

# STUDIES IN NEOTROPICAL PALEOBOTANY. I. THE OLIGOCENE COMMUNITIES OF PUERTO RICO<sup>1</sup>

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## ABSTRACT

Studies are being made of plant microfossils from seven Tertiary formations in Mexico, Panama, and Puerto Rico. The Puerto Rican samples from the Oligocene San Sebastian Formation have yielded 165 morphological forms; 44 have been identified, and 15 of these have no previously known fossil record. Community types include a coastal, brackish-water assemblage of *Rhizophora* and *Pelliciera*, an upland tropical to subtropical community, and an arboreal cool-temperate community of *Fagus*, *Liquidambar*, and *Nyssa*. Of the 44 genera identified, 31 presently grow in Puerto Rico, three grow on other islands of the Antilles, seven are found in ecologically comparable habitats elsewhere in Latin America, and only the three temperate trees require habitats not presently available on the island. The temperate element suggests altitudes greater than those of today, and recently available geological data reveal the presence of Oligocene highlands of 13,000 to 15,000 feet elevation. These would be sufficient to provide cool-temperate conditions in an insular environment at 18 degrees north. Ancestral Puerto Rico (Hispaniola, Puerto Rico, and the Virgin Islands) provided an effective landbridge between northern South America, the West Indies, and Mexico (Yucatan). However, the Oligocene seas extended across at least part of peninsula Florida and up to 120 miles inland along the Texas Gulf Coast; thus the barrier to migration from the Antilles into southeastern North America was probably greater than at present. Of the 44 genera identified all have affinities with northern South America, eastern Mexico, and the Antilles; and none have exclusive affinities with the vegetation of southeastern North America. Studies from Panama and Veracruz, Mexico, suggest tropical elements in the modern and fossil floras of southeastern North America were introduced along an Isthmian-coastal Mexico route during the early Tertiary or subsequently through long-distant dispersal into tropical outliers (southern peninsula Florida).

The tropics are generally recognized as an important center for biological diversity, and a number of studies are underway dealing with the systematics, ecology, and evolutionary aspects of tropical plant communities. The more recent

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These studies began while one of the authors (AG) was a postdoctoral fellow in the Evolutionary Biology Program, Harvard University. Sincere gratitude is expressed to Reed C. Rollins, Director of the Program, and especially to Professor Elso Barghoorn in whose laboratory the work was initiated. R. A. Howard was frequently consulted about the modern vegetation of Puerto Rico. Rolla and Alice Tryon provided helpful suggestions on the ferns, and G. J. Gastony supplied ecological and floristic data for Pico Duarte, Dominican Republic. Other individuals providing information on special plant groups are Donald E. Stone (*Engelhardia*), Peter H. Raven (*Hauya*), and Grady L. Webster (*Alchornia*, *Tetrorchidium*). The authors also acknowledge courtesies extended by the staff of the herbaria and libraries of Harvard University, the University of Michigan, and the Smithsonian Institution. On matters of geology, W. H. Monroe, Othmar Tobisch, and especially R. P. Briggs, U.S. Geological Survey, San Juan provided much helpful information.

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paleobotanical record also constitutes an important source of data relating to the environment and environmental change under which the biota has diversified, pathways of migration, interchange between the North and South American communities, and former occurrences of species now disjunct or allopatric in distribution. Unfortunately even less is known about the geologic history of tropical American biotas than the modern associations. Although several recent studies on Cenozoic deposits have been made (Bartlett, 1967; Cogwill *et al.*, 1966; Gonzalez-Guzman, 1967; Heusser, 1961, 1964, 1966; Germeraad, Hopping & Muller, 1968; Langenheim, Hackner & Bartlett, 1967; Tsukada & Deevey, 1967; Hammen, 1963, 1964; Hammen & Gonzalez, 1960; Hammen & Wijmstra, 1964; reviews by Archangelsky, 1968; Menendez, 1969) and others are underway, there still have been more Tertiary paleobotanical studies made in the western United States than in the rest of the Western Hemisphere south of the United States. Indeed there have been more revisions of fossil floras of the Columbia Plateau than combined Tertiary paleobotanical studies in the countries of Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, the Guianas, Ecuador, Paraguay, Uruguay, and Peru.

Among deterrents to traditional (*viz.*, megafossils) paleobotanical research in tropical regions have been the difficulty and uncertainty of obtaining researchable materials. Geologic maps may reveal the location of fine-grain, black shales associated with coal seams or continental shales of volcanic origin, but there is no certainty these beds will yield plant megafossils. However, rock types such as peat, lignite, and coal commonly contain pollen and spores. A total of 281 samples have been collected from Tertiary formations in Mexico, Panama, and Puerto Rico (Fig. 1), and about 75% yielded well-preserved plant microfossils. In many Latin American countries these rock types are important as a low-cost source of fuel, and consequently their age and distribution is frequently better known than for economically less important deposits. Thus the initial phases of these investigations concentrate on the palynology of lignites, while reconnaissance continues for supplementary megafossil sites.

The practical necessity of beginning with palynology and lignites presents difficulties that affect interpretation of the data. Fossil pollen and spores most commonly can be identified only to genus—in a few cases to species, but in others only to family. Further, study of either the micro- or megafossil community provides only a part of the potential species composition. In a Miocene flora from southeastern Oregon (Graham, 1963, 1965*a*), 16 genera (27% of the flora) were represented as microfossils but were absent from the megafossil assemblage, and 10 genera (17%) were found only as megafossils. Since the species list is the basis for interpretation of fossil floras, the necessity of considering only the palynology of these Latin American deposits is a limiting factor of some consequence. Another problem is facies control of the microfossil composition. Lignites in warm-temperate regions are formed under brackish-water, coastal environments and commonly contain 75–95% *Rhizophora* pollen. Thus the samples are biased toward strand vegetation and may provide little data on communities removed from the basin of deposition. This difficulty recently has been overcome to some



extent in the Panamanian and Puerto Rican deposits by obtaining pollen-bearing samples of different lithologies associated with the lignites. Other problems include the inadequacy of existing reference collections for identification purposes and the lack of pertinent literature on the distribution and ecology of tropical plants once the microfossils have been identified. Although these difficulties presently require conservative interpretation of data and tentative conclusions, even preliminary investigations can yield data significant in comparison to our present state of knowledge.

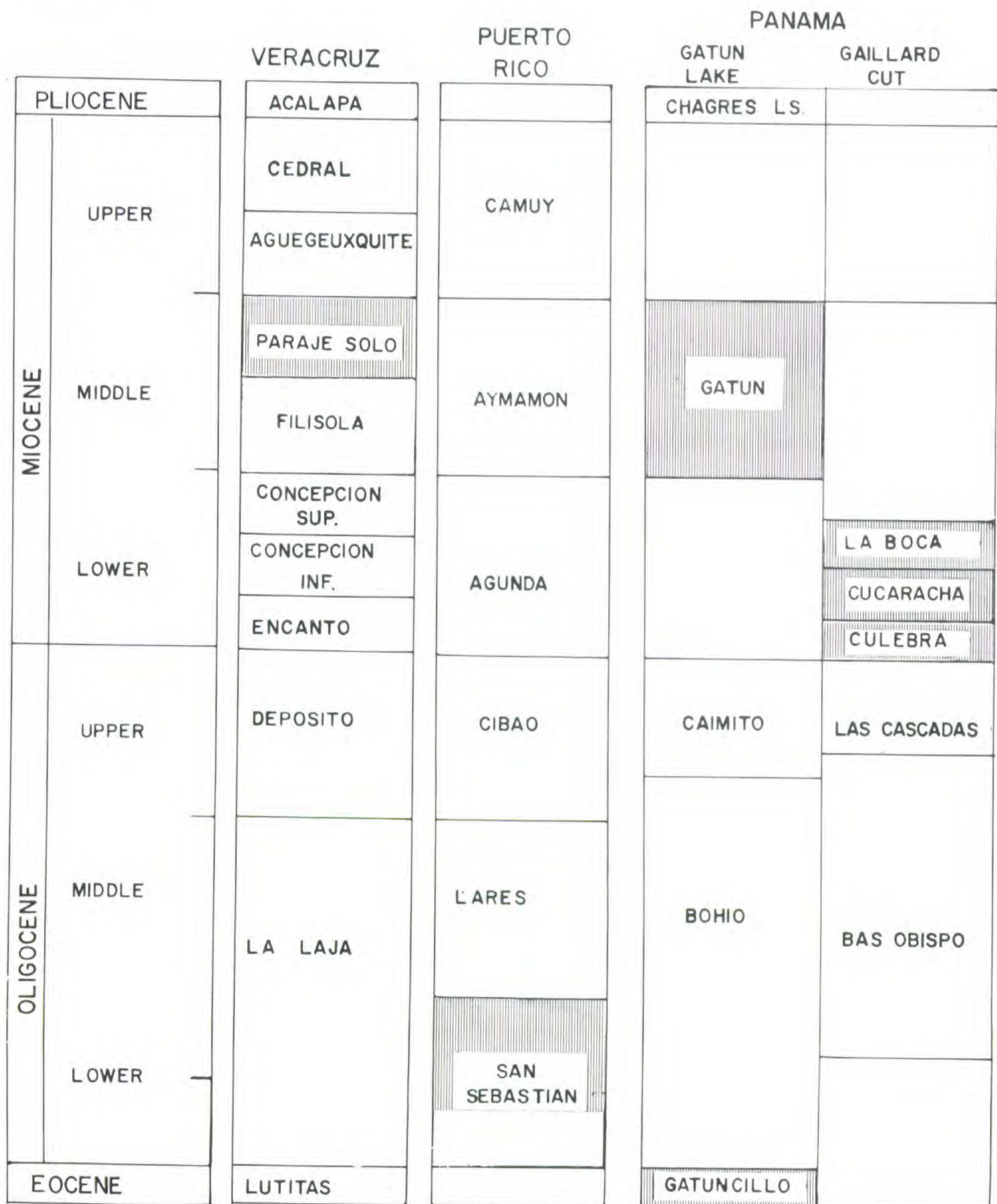


FIGURE 1.—General stratigraphic position of Tertiary formations in northern Latin America included as a part of "Studies in Neotropical Paleobotany."



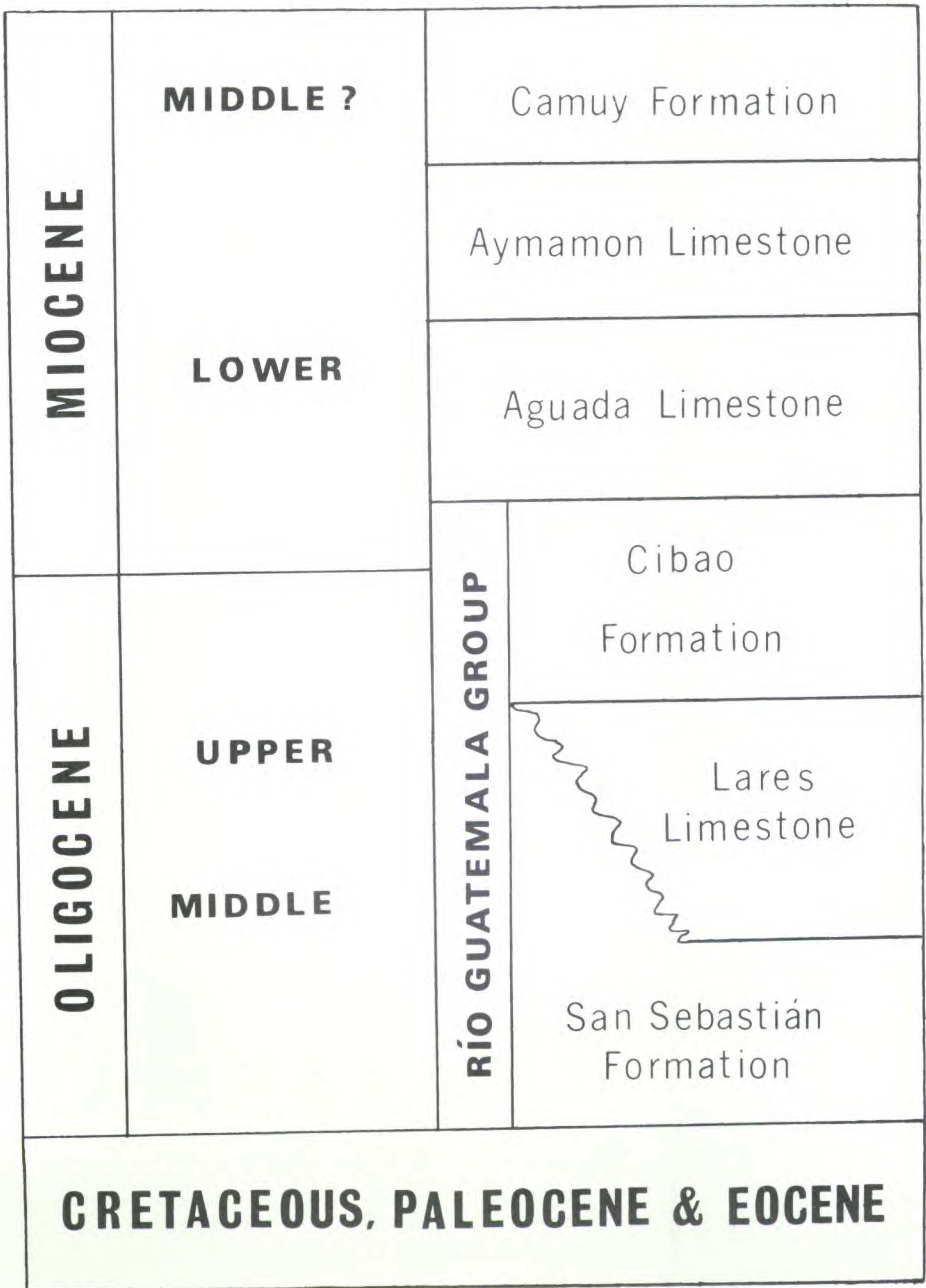


FIGURE 2.—Stratigraphic relationships of the San Sebastian Formation to other Oligocene and Miocene strata of Puerto Rico.



There is no published palynological information dealing with the Tertiary vegetation of the Antilles, and only a single paper (Hollick, 1928) treats plant megafossils. The usefulness of such data to an understanding of vegetational history in northern Latin America, and the origin of certain floristic affinities between North and South America is evident from the position of the islands. Forming an arc extending nearly from the Yucatan Peninsula eastward toward the Florida Keys and Bahama Islands, then curving south to the island of Trinidad, the islands are geographically suited to act as a land bridge between North and South American biotas.

Puerto Rico is the smallest and most easterly island of the Greater Antilles, located between  $18^{\circ}$  and  $18^{\circ} 30'$  north and  $65^{\circ} 30'$  and  $67^{\circ} 30'$  west, with an area of 3,435 square miles. Average rainfall for the island ranges from over 180 inches in the eastern Cordillera to about 10 inches along the southwestern coast. Mean annual temperatures range from  $78^{\circ}$  F along the south coast to  $70^{\circ}$  F in the mountains. Recent accounts of the climatology and physiography of Puerto Rico are given by Banyon (1968, 1969), Pagney (1966), and Pico (1950, 1963). There are numerous accounts of the geology of Puerto Rico including those of Berkey (1915, 1919), Butterlin (1956), Hubbard (1920, 1923), Maury (1929), Meyerhoff (1933), Mitchell (1954), Zapp, *et al.* (1948), Kaye (1956), and Mattson (1967).

The study sites are located in the northwestern portion of Puerto Rico and have a base of tuffaceous sandstone and siltstone of Cretaceous, Paleocene, and Eocene age (Monroe, 1968). The San Sebastian Formation lies unconformably on this basement of Eocene strata and outcrops at several locations. The formation ranges in thickness from less than 1 m to 155 m and consists of sand and gravel, lignites and lignitic clays, and thin lenses of clay and very sandy clayey limestones. Above lies the Lares Limestone, and in places it becomes a facies equivalent of the San Sebastian Formation. The relationship between the Lower and Middle Tertiary formations of Puerto Rico in the vicinity of the collecting sites is shown in Fig. 2 (Briggs; Monroe, personal communication, 1969). The San Sebastian and Lares Limestones are considered Middle Oligocene, and thus the microfossils represent vegetation existing within the Greater Antillean Arc approximately 45 million years ago.

#### MATERIALS AND METHODS

Lignitic clays and coal deposits containing well-preserved plant microfossils were obtained from outcrops of the Oligocene San Sebastian Formation, recently mapped by Briggs and Akers (1965). A collection of 50 samples was made from three localities designated PRL (Puerto Rican Lignites) A, B, and C (Fig. 3).

Locality PRL-A is on a small east-facing slope at the junction of Puerto Rican Highways 111 and 124, just west of Lares at the 35.3 km marker. The slope pinches out from north to south from a width of 20–22 feet to less than one foot. Two thin beds, 10 in. thick, of dark organic sediment are exposed. The upper bed is lignitic clay, with occasional lignite or brown coal interbedded in small quantities. The lower bed is a coarse steel grey lignitic sandstone with abundant invertebrate remains (calcareous shells). Samples 1–10 were collected from the upper lignitic clay, and samples 11–13 were made from the lower lignitic sandstone. All samples contained plant microfossils.

Locality PRL-B is on a new east-facing slope resulting from construction of a by-pass around the town of Lares. This by-pass to Highway 111 runs approximately NNE and is



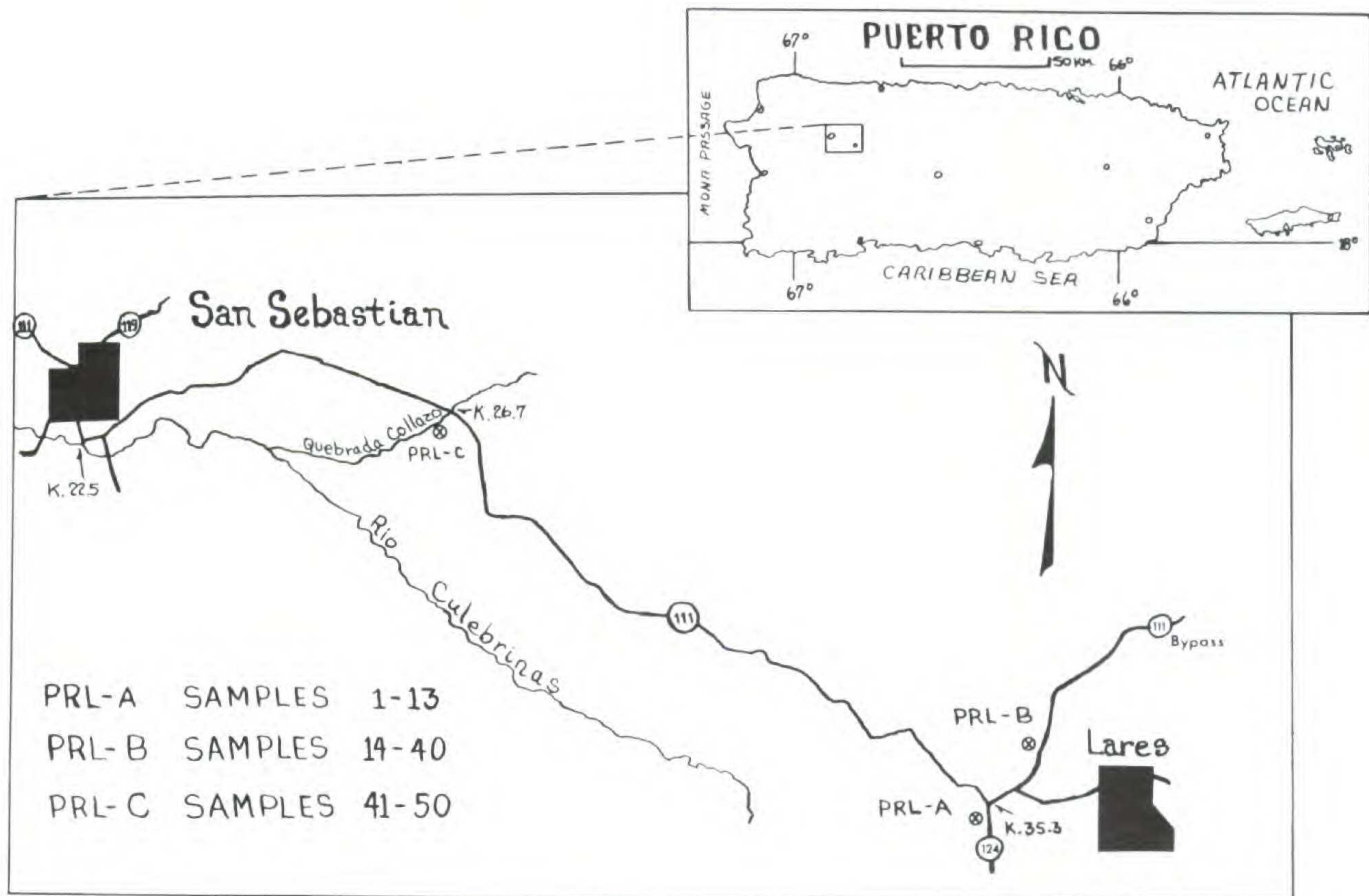


FIGURE 3.—Index map of Puerto Rican lignite localities.

adjacent to the east-facing slope. Samples 14–40 were collected from this locality (Fig. 4). The bluff is 40–45 feet high from the road base and is interbedded with alternating coal, coaly lignite, and lignitic clay.

Locality PRL-C is on the Collazo Quebrada at the base of the second falls below the San Sebastian-Lares bridge, at the 26.7 km marker. The bridge is approximately 4.2 km from the town of San Sebastian on Highway 111. This is the same site mentioned by Hollick (1928) as "Collazo River, near (or 'at') base of second falls below Carretara bridge." Samples 41–50 were collected from a lignitic clay about one foot thick containing abundant cuticles which curl from the surface of the rock upon drying; the matrix readily crumbles. Lenses of lignitic clay were also described from the base of the first falls (Hubbard, 1923) and at several other sites, but slumping and accumulation of debris have obscured these localities.

Samples were cleaned to expose unoxidized surfaces, macerated and covered with 48% HF for 24 hours to remove silicates. This was followed by 10% HCl to remove carbonates. Schultze Solution was used for 15–20 minutes to oxidize organic constituents. Separation of organic and residual inorganic fractions was by heavy-liquid flotation using  $ZnBr_2$  adjusted to a specific gravity of 1.8 and centrifuged at 2000 rpm for one-half hour. The float fraction was acetolized and mounted unstained in glycerine jelly. Fifteen slides from each sample were prepared and sealed with diaphane. Photographs were made with a Wild microscope equipped with a Nikon 35 mm camera and were mounted on Burroughs Y-9 Unisort Analysis Cards for reference.

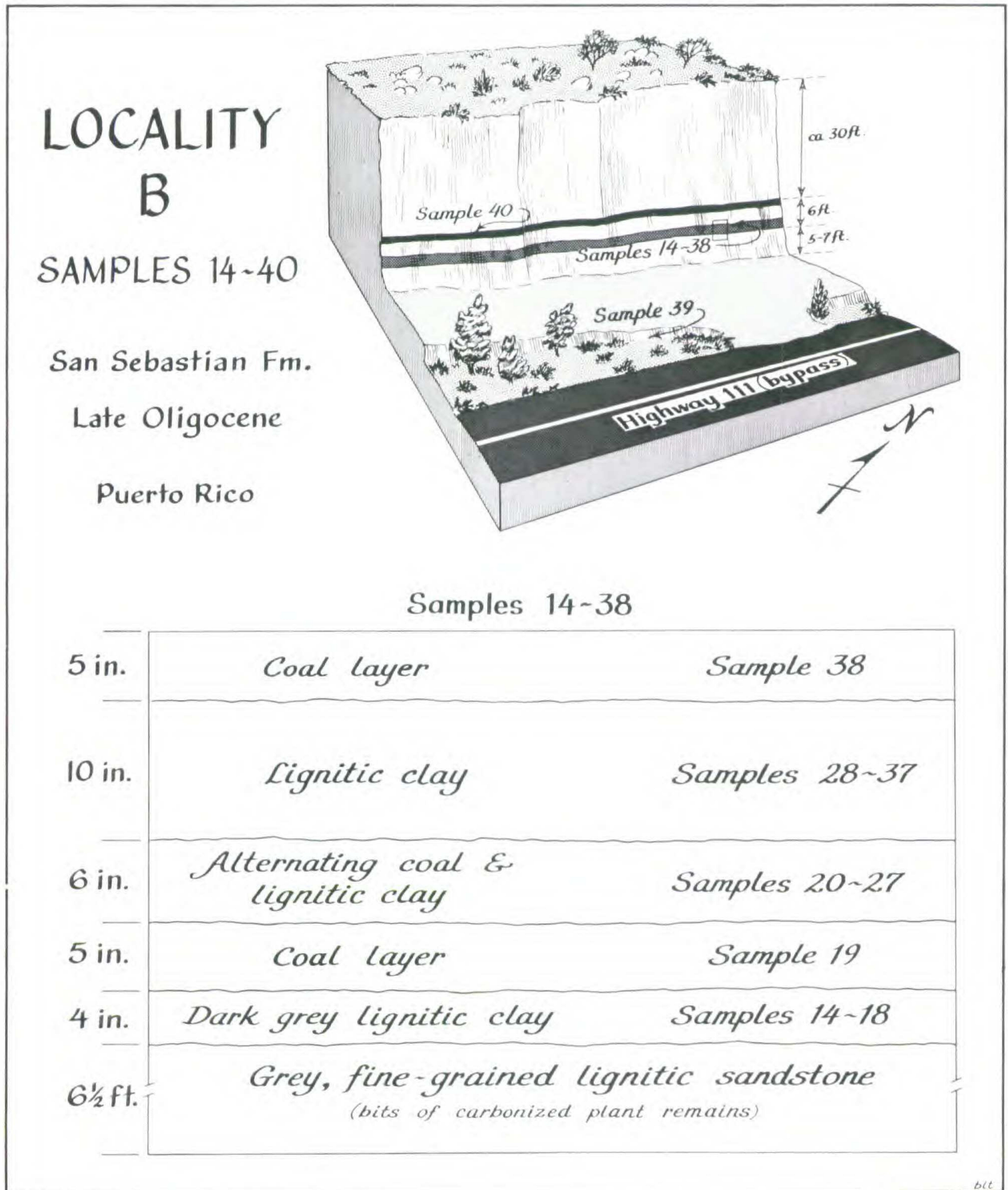
Comparison of fossil types with modern material was made from the reference collection of about 12,000 species at Kent State University. Additional collections of modern material were made as necessary from specimens in US. All slides from Locality C and three to five slides from Localities A and B were scanned for morphological types. Estimates of relative abundance were made by tabulating the first 200 recognizable types, and these are listed as rare (0.5% or less), common (0.5–15%), or abundant (greater than 15%).

Once the fossils were identified, distribution maps were prepared showing the range of the modern counterparts. Distribution and ecological data were obtained from the literature (e.g., Standley, 1920–1926, 1928; Little & Wadsworth, 1964; Alain, 1963, 1968; Gleason



& Cook, 1926; Howard, 1962, 1966; Allen, 1956) and from herbarium sheets at US and GH.

All slides, photomicrographs, and other data relevant to the study are on deposit at the Palynology Laboratory, Kent State University.





## SYSTEMATICS

A total of 165 morphological types of pollen and spores were recovered from the San Sebastian Formation. From this assemblage 44 (ca. 25%) have been identified to genus. In the following discussion the palynomorphs are cited according to locality (A, B, or C) and sample number (1–50). The photomicrographs are cited according to locality, sample number, and slide number (1–15), and coordinates of the England Slide Finder are also given. A summary of relative abundance is given in Table 1 and the species composition of the San Sebastian microflora in Table 2. Detailed descriptions are deferred to a later publication where the microfossils will be given formal taxonomic status.

*Lycopodium* (Fig. 5–6)

The genus *Lycopodium* consists of approximately 100 species widely distributed throughout tropical and temperate regions of the world. The spores of many temperate forms and those most frequently reported from Cenozoic deposits in the Northern Hemisphere are characterized by a distinct reticulum on the distal surface. Certain tropical species differ, however, in having slightly protruding, broadly blunt apices and/or a rugulate to less distinct reticulate sculpture pattern. The spores of *Lycopodium* Type A are similar to those of *L. carolinianum*. They were recovered from samples C-43 and C-50, with an abundance of 0.5%.

The spores of *Lycopodium* Type B are most similar to the modern *L. serratum*. Although we did not see collections of the plant from Puerto Rico, it does occur on Cuba and Haiti. Single specimens were recovered from samples C-48 and C-50.

*Selaginella* (Fig. 7)

Members of the genus *Selaginella* number about 700 species and are chiefly tropical in distribution, with a few ranging into temperate regions. At least three species are recorded from Puerto Rico, *S. laxifolia*, *S. krugii*, and *S. substipitata*. The spores are rare in the San Sebastian microflora and occur at Localities B and C.

*Cyathea* (Fig. 8)

The genus *Cyathea* is a tropical to subtropical assemblage of approximately 800 species. It is an arborescent fern of the wet tropics especially in the mountainous regions from Mexico to Chile. In the Antilles it occurs on all the islands and is represented by about 35 species including *C. arborea*, *C. borinquena*, and *C. pubescens*. *Cyathea arborea* is the most widespread and is abundant on Puerto Rico. The plants are common secondary invaders of impoverished soils in damp climates, especially at lower altitudes (Richards, 1966: 398).

The fossil spores range in size from 35 to 55 $\mu$ , suggesting more than one species may be represented. They are present in Locality B, samples 15, 19, 25, and 33 with an abundance of 0.5–1.5%, and in Locality C, samples 41, 43, and 50 with an abundance of 0.5–1.0%.



TABLE 1. Per cent composition of identified taxa from San Sebastian Formation (Oligocene), Puerto Rico (based on 200 grains counted). P = present.

Taxon	Locality A						Locality B					Locality C				
	3	4	8	10	12	13	15	19	25	33	40	41	43	45	48	50
<i>Lycopodium A</i>													.5			.5
<i>Lycopodium B</i>															P	P
<i>Selaginella</i>												P			P	P
<i>Cyathea</i>							1	.5	1.5	.5		.5	1			.5
<i>Hemitelia</i> ( <i>Cnemidaria</i> )															P	
<i>Jamesonia</i> ( <i>Eriosorus</i> )																
<i>Pteris (A,B,C)</i>							5	.5		.5				P		
<i>Podocarpus</i>												P		P		
<i>Abutilon</i>																
<i>Acacia</i>					.5								.5	P		
<i>Aetanthus</i>																
<i>Alchornea</i>	.5				1	1	1	.5	1			1	.5	.5	.5	.5
<i>Bernoullia</i>												.5	.5	5	2.5	1
<i>Bombax</i>																
<i>Brunellia</i>										P			1		1.5	
<i>Bursera</i>																
<i>Casearia</i>																
<i>Catostemma</i>					.5							P	2.5	1	P	1
<i>Chrysophyllum</i>									.5			P				
<i>Corynostylis</i>								.5					.5			.5
<i>Dendropanax</i>															P	
<i>Engelhardia</i>	1.5		1		2	2.5	15	3	2.5	.5	.5	44.5	31	54	41.5	37
<i>Eugenia</i>												.5		P	.5	
<i>Fagus</i>	1															
<i>Faramea</i>									1.5			P				
<i>Guarea</i>												.5	P	P	.5	
<i>Hauya</i>													.5		P	
<i>Ilex</i>																
<i>Jacaranda</i>																
<i>Liquidambar</i>													1.5	.5	2	.5
<i>Marcgravia</i>																
<i>Merremia</i>													.5			
<i>Myrica</i>																
<i>Norantea</i>																P
<i>Nyssa</i>	.5											.5	1.5		4.5	.5
<i>Oxalis</i>																
<i>Pelliciera</i>		2	1	1	1	P									P	
<i>Pleodendron</i>												.5	.5			.5
<i>Rauwolfia</i>																
<i>Rhizophora</i>	89	95	96	95.5	47.5	36	1	77	61.5		71	.5	.5			1.5
<i>Salix</i>													1		.5	
<i>Tecoma</i>																
<i>Tetrorchidium</i>					.5		1.5	2		.5		P	3	1	1	.5
<i>Tournefortia</i>					P											
<i>Zanthoxylum</i>							.5					1.5				P
Monolete Fern Spores (Poly- podiaceae)					2	6.5	9	5	5	30	5	12	18	10	8	5
Trilete Fern Spores	2				9	16	10	5	4	10	10	8	12	13	5	7
Palmae	1	2			3.5	3.5	8	5	7	50	2	5	15	9	12	12
Unidentified	4.5	1	2	3.5	32.5	34.5	48	1	15.5	8.5	11	24.5	8	6	19.5	31.5



TABLE 2. Systematic listing of identified genera occurring in the San Sebastian Formation, Puerto Rico.

Family: Lycopodiaceae	Genus: <i>Liquidambar</i>	Family: Violaceae
Genus: <i>Lycopodium</i>	Family: Oxalidaceae	Genus: <i>Corynostylis</i>
Family: Selaginellaceae	Genus: <i>Oxalis</i>	Family: Flacourtiaceae
Genus: <i>Selaginella</i>	Family: Rutaceae	Genus: <i>Casearia</i>
Family: Cyatheaceae	Genus: <i>Zanthoxylum</i>	Family: Rhizophoraceae
Genus: <i>Cyathea</i>	Family: Burseraceae	Genus: <i>Rhizophora</i>
Genus: <i>Hemitelia</i> ( <i>Cnemidaria</i> )	Genus: <i>Bursera</i>	Family: Myrtaceae
Family: Gymnogrammaceae	Family: Meliaceae	Genus: <i>Eugenia</i>
Genus: <i>Jamesonia</i> ( <i>Eriosorus</i> )	Genus: <i>Guarea</i>	Family: Onagraceae
Family: Polypodiaceae	Family: Euphorbiaceae	Genus: <i>Hauya</i>
Genus: <i>Pteris</i>	Genus: <i>Alchornea</i>	Family: Araliaceae
Family: Podocarpaceae	Genus: <i>Tetrorchidium</i>	Genus: <i>Dendropanax</i>
Genus: <i>Podocarpus</i>	Family: Aquifoliaceae	Family: Nyssaceae
Family: Salicaceae	Genus: <i>Ilex</i>	Genus: <i>Nyssa</i>
Genus: <i>Salix</i>	Family: Malvaceae	Family: Sapotaceae
Family: Myricaceae	Genus: <i>Abutilon</i>	Genus: <i>Chrysophyllum</i>
Genus: <i>Myrica</i>	Family: Bombacaceae	Family: Apocynaceae
Family: Juglandaceae	Genus: <i>Bombax</i>	Genus: <i>Rauwolfia</i>
Genus: <i>Engelhardia</i>	Genus: <i>Catostemma</i>	Family: Convolvulaceae
Family: Fagaceae	Genus: <i>Bernoullia</i>	Genus: <i>Merremia</i>
Genus: <i>Fagus</i>	Family: <i>Marcgraviaceae</i>	Family: Boraginaceae
Family: Loranthaceae	Genus: <i>Marcgravia</i>	Genus: <i>Tournefortia</i>
Genus: <i>Aetanthus</i>	Genus: <i>Norantea</i>	Family: Bignoniaceae
Family: Brunelliaceae	Family: Theaceae	Genus: <i>Jacaranda</i>
Genus: <i>Brunellia</i>	Genus: <i>Pelliciera</i>	Genus: <i>Tecoma</i>
Family: Hamamelidaceae	Family: Canellaceae	Family: Rubiaceae
	Genus: <i>Pleodendron</i>	Genus: <i>Faramea</i>

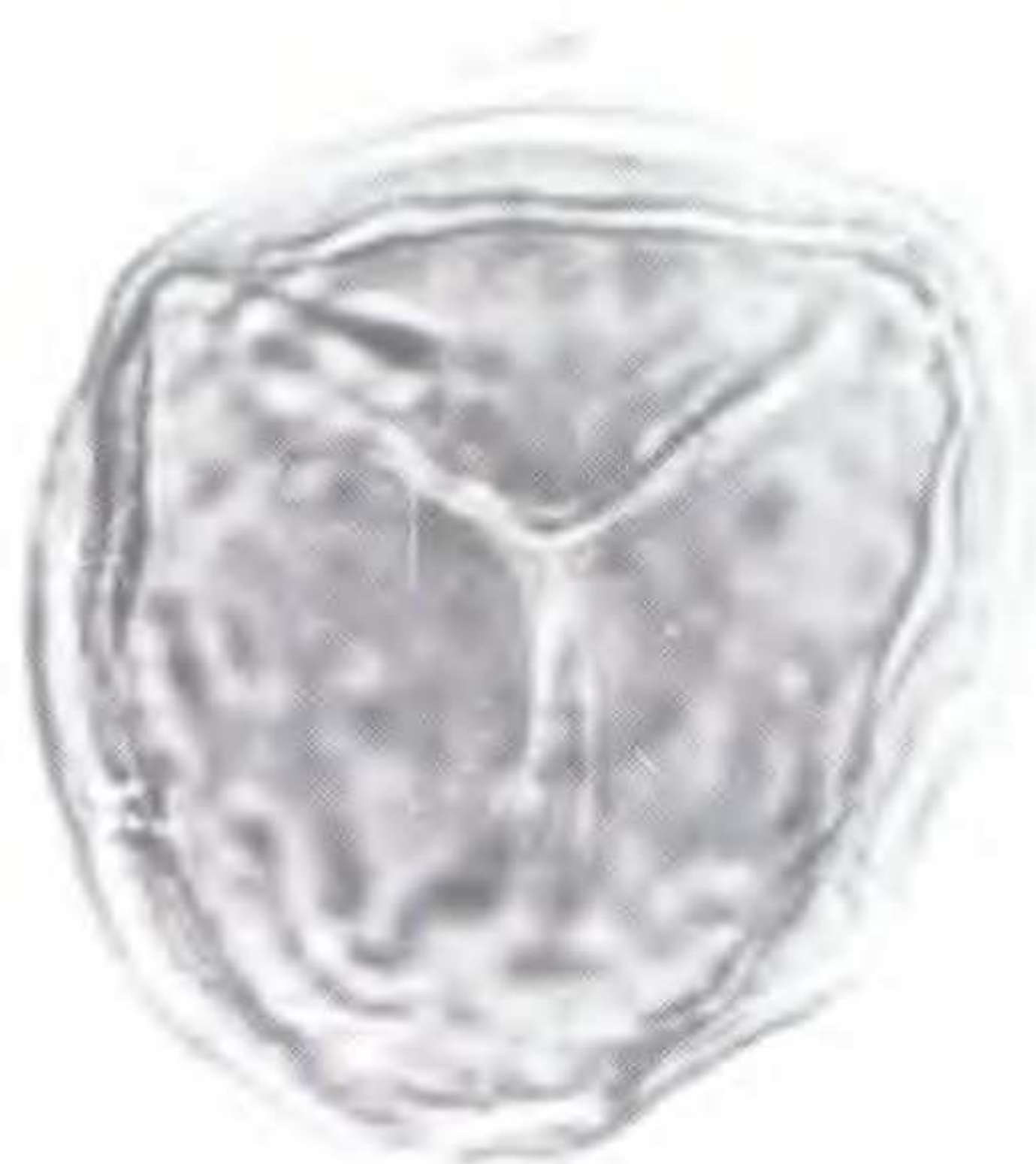
Previous reports of fossil spores of *Cyathea* include Hammen and Gonzalez (1960) from the Pleistocene of Colombia and Hammen (1963) from the Quaternary of Guyana. Megafossils have been reported by Berry (1922: 119) from the Miocene of Chile, Hollick and Berry (1924) from the Pliocene of Bahía, Brazil, and Pabst (1968) from the Chuckanut Formation (Paleocene?) of northwestern Washington.

#### *Hemitelia* (*Cnemidaria*; Fig. 9)

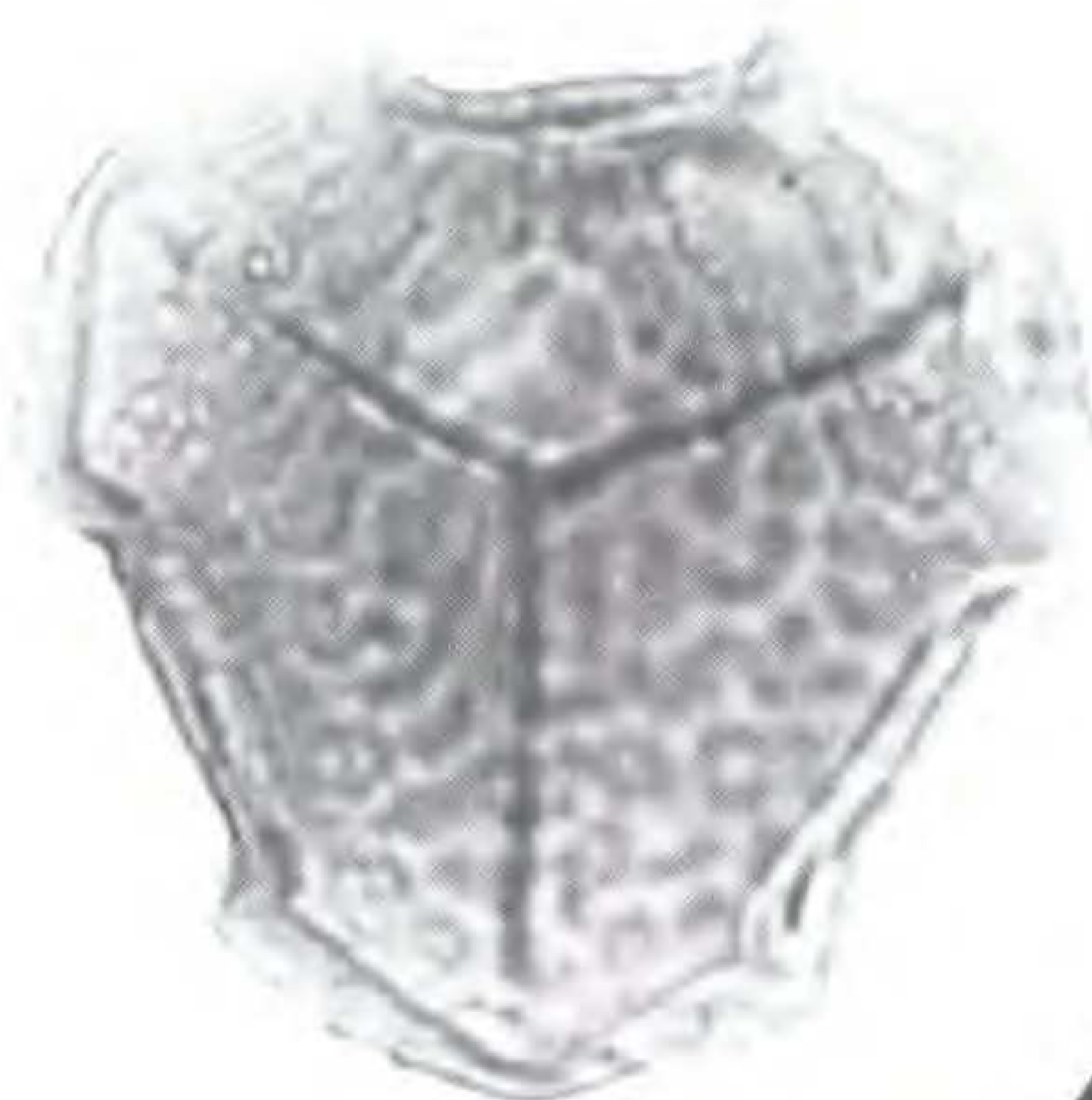
The taxonomy of the tree ferns is currently being revised, and there are nomenclatural differences between the older and newer systems. According to some treatments the arborescent ferns belong to the genus *Cyathea*, while others recognize a number of genera. In a forthcoming revision ferns previously recognized as *Hemitelia* will be called *Cnemidaria* (R. Tryon, personal communication, 1969). The plants are common to moist tropical mountains, and three species, including *H. horrida*, are native to Puerto Rico. They are occasional to rare, however, and usually do not reach tree size as do species of *Cyathea* (Little & Wadsworth, 1964). The genus is pantropical in distribution, and about 40 species are recognized (Fig. 69).

A single specimen of *Hemitelia* was found in sample C-48. Other reports are those of Hammen and Gonzalez (1960) from the Pleistocene and Holocene of Colombia, and the spores are common in our samples from the Miocene Paraje





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6



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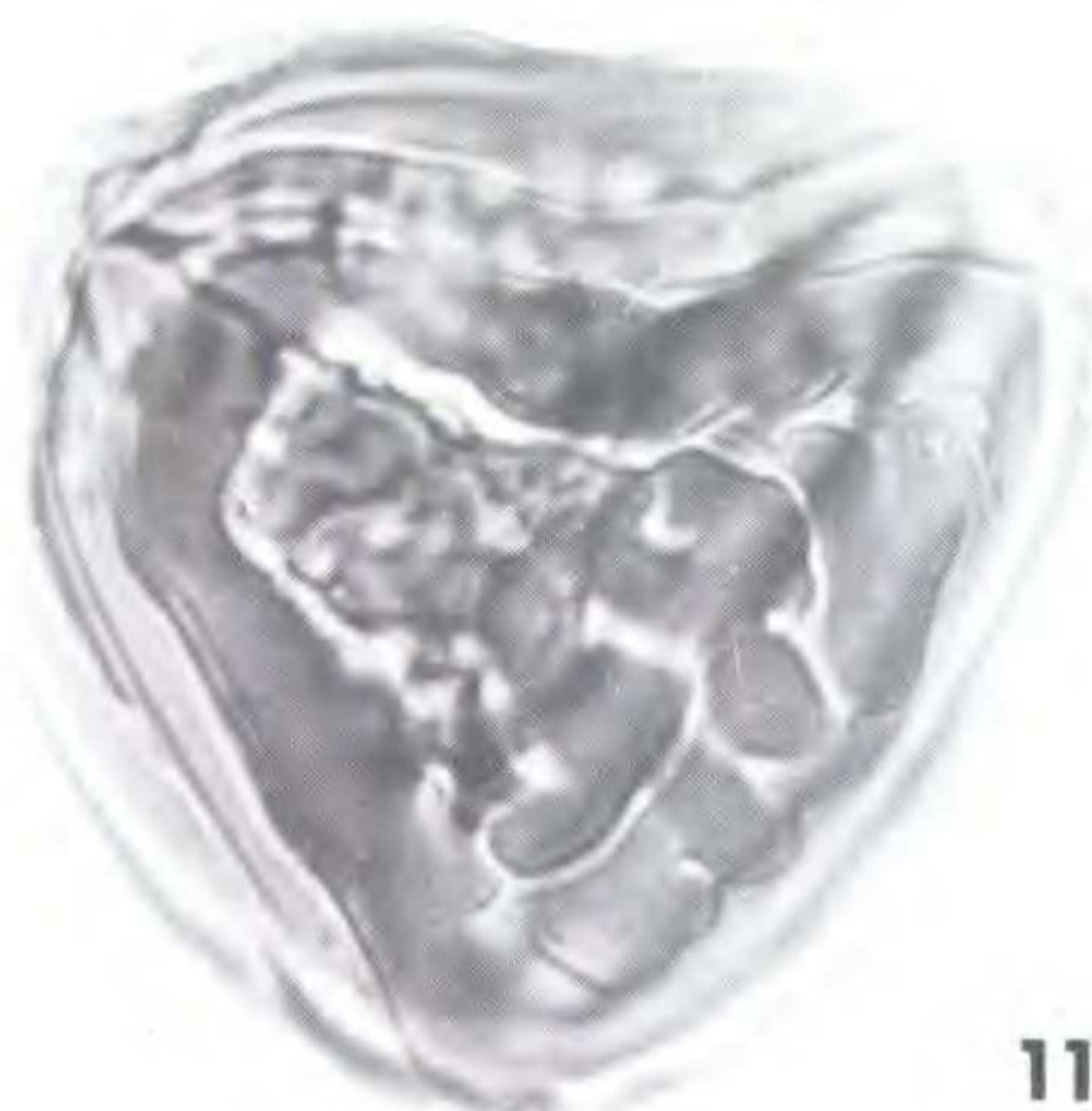
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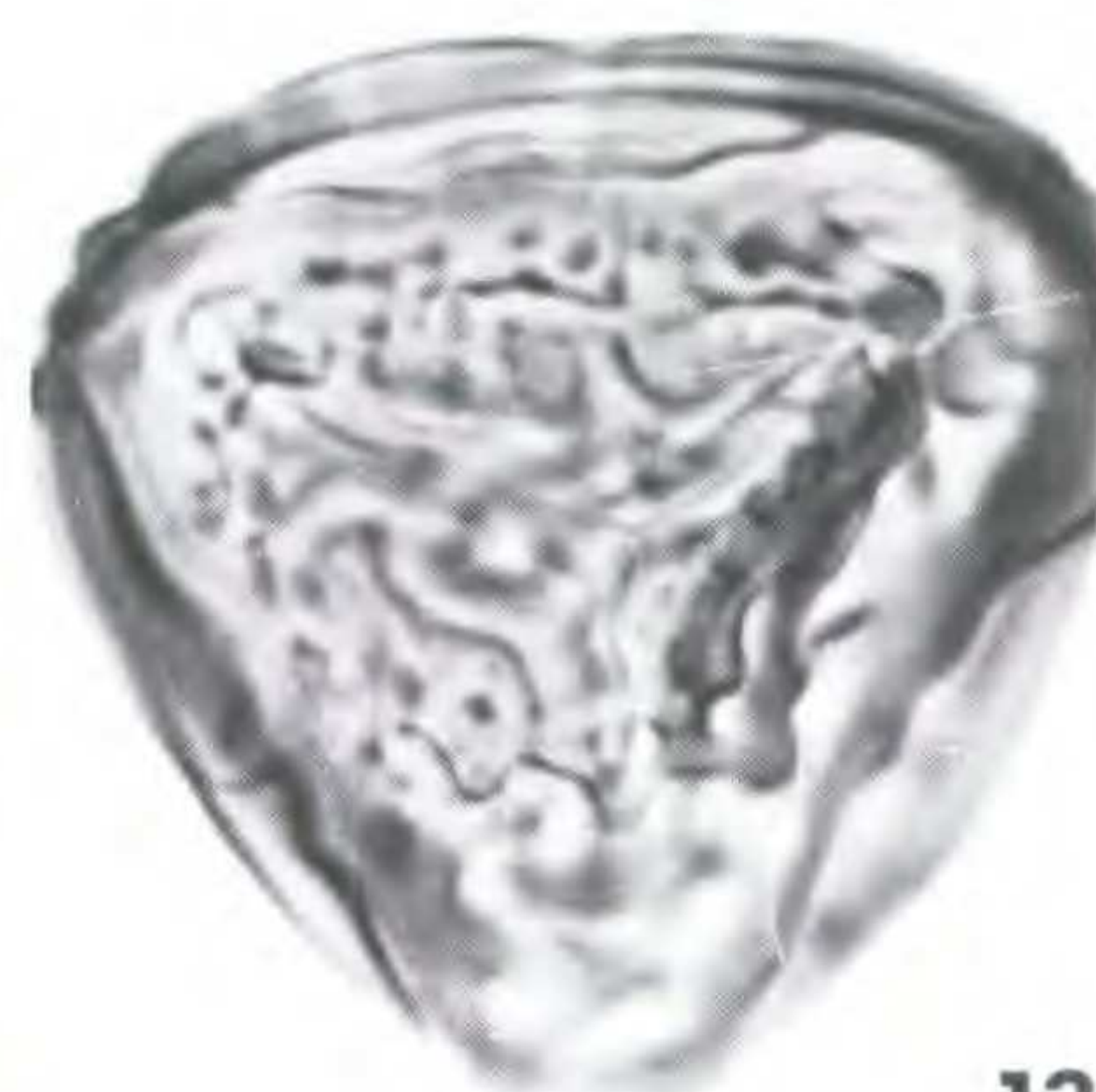
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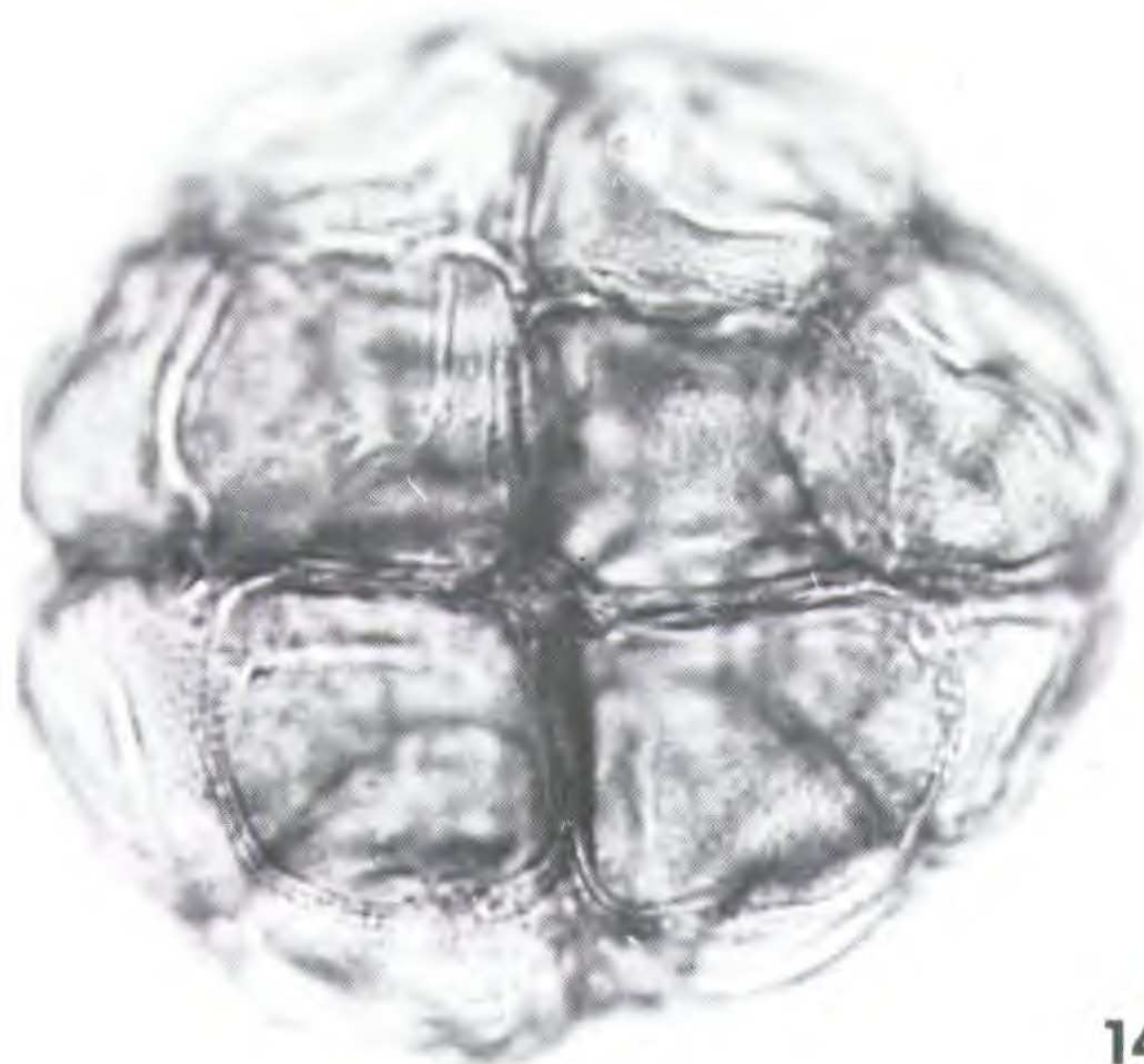
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Solo Formation of Veracruz, Mexico. Wolfe (personal communication, 1969) has megafossils, probably related to Asiatic forms, from Tertiary material in Alaska. Hollick and Berry (1924) described fossil fronds from the late Tertiary of Bahía, Brazil, as *H. branneri*. It was compared to *H. grandifolia* which is present today in the Antilles and tropical South America. Hollick (1928) also reported fronds of *H. branneri* from the Collazo Shales of Puerto Rico.

#### *Jamesonia* (Fig. 10)

The spores of *Jamesonia* are similar to *Eriosorus*, and the two genera are closely related (A. Tryon, personal communication, 1969). With limited fossil material generic identification is tentative, although the spore is most similar to *Jamesonia* among the genera represented in our reference collection. *Jamesonia* consists of about 19 species distributed from southern Mexico to central Bolivia and Brazil. It is a high altitude plant (1,500–5,000 m) of the paramos or other cool, wet highlands (Tryon, 1962); it characteristically grows at elevations higher than *Eriosorus*.

The genus *Eriosorus* consists of about 30 species occurring from Andean South America, Brazil, Bolivia, and on the sandstone massifs of Venezuela north to Guerrero, Mexico. *Eriosorus hispidulus* grows on the isolated Atlantic island of Tristan da Cunha (Tryon, 1966) and on El Yunque, Puerto Rico. It is a member of the wet cloud forest vegetation growing most commonly at elevations above 2,000 m.

A single spore of *Jamesonia* (or *Eriosorus*) was recovered from sample C-49. Spores of *Jamesonia* are reported from the Pleistocene and Holocene of Columbia (Hammen & Gonzalez, 1960), and *Eriosorus* is known from the Pleistocene of Tristan da Cunha (Hafsten, 1960).

#### *Pteris* (Fig. 11–13)

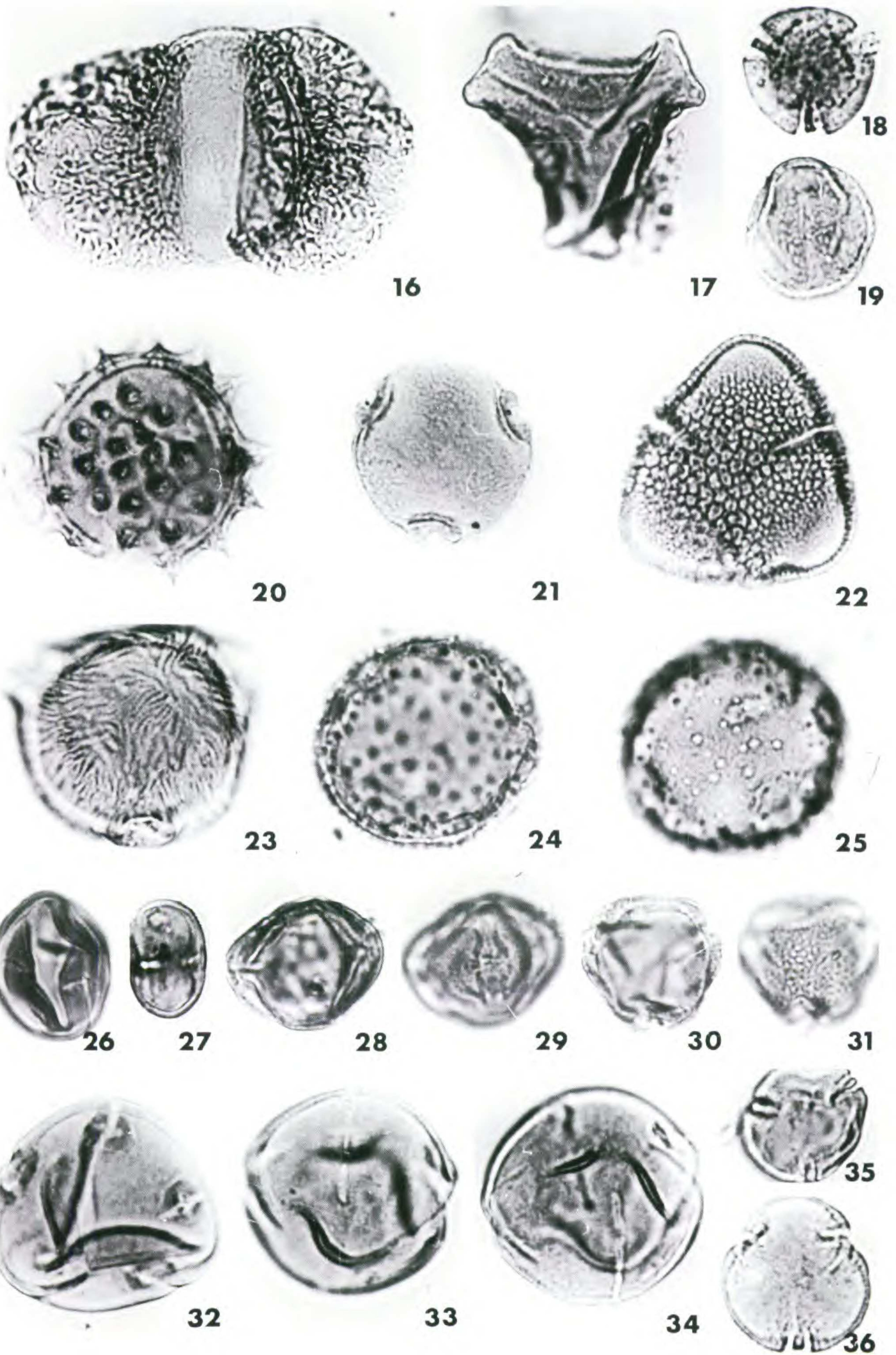
The spores of *Pteris* are common in the San Sebastian Formation. Several species are probably represented. Three relatively distinct types can be recognized, based on differences in sculptural elements on the distal surface. In Type A the sculpturing elements are a series of irregularly distributed sharp ridges; in Type B, low rounded ridges; and in Type C, verrucae.

The genus consists of about 250 species. At least some grow under relatively xerophytic conditions and may be primary invaders in dry barren regions (Richards, 1966: 271). Spores of *Pteris* are common at Localities B and C, being most abundant in samples C-43, 45, and 50, where they represent as much as 5%



FIGURES 5–15.—San Sebastian (Oligocene) microfossils, Puerto Rico. — 5. *Lycopodium* Type A, 40 $\mu$  (C-50, 1; ESF Y-35). — 6. *Lycopodium* Type B, 40 $\mu$  (C-50, 15; ESF O-21,3). — 7. *Selaginella*, 28 $\mu$  (C-48,1; ESF N-28). — 8. *Cyathea*, 33 $\mu$  (C-43,15; ESF B-45). — 9. *Hemitelia*, 42 $\mu$  (C-48,1; ESF O-31,1). — 10. *Jamesonia* (*Eriosorus*), 44 $\mu$  (C-49,1; ESF K-25,2). — 11. *Pteris* Type A, 54 $\mu$  (C-42,1; ESF S-38,4). — 12. *Pteris* Type B, 43 $\mu$  (C-44,5; ESF L-26). — 13. *Pteris* Type C, 45 $\mu$  (C-46,2; ESF K-28,4). — 14. *Acacia*, 72 $\mu$  (C-45,10; ESF J-38,3). — 15. *Bernoullia*, 59 $\mu$  (C-48,10; ESF G-30).







of the total assemblage. Spores similar to *Pteris* have been reported by Hammen and Gonzalez (1960) from the Pleistocene of Colombia as *Triletes* "tipo J."

*Podocarpus* (Fig. 16)

The genus *Podocarpus* consists of about 100 species distributed primarily in the Southern Hemisphere. Sixteen species are known from Mexico, Central America, and the Antilles (Fig. 70). Among these, *P. coriaceus* occurs on Puerto Rico and is the only native conifer. The plants grow in high-mountain, tropical forests, although they are more abundant near the bottom of slopes in moister soil (Gleason & Cook, 1926: 115). It is a medium-size tree (ca. 10 m tall) and produces pollen nearly throughout the year (Little & Wadsworth, 1964).

*Podocarpus* pollen is rare, in the San Sebastian Formation, with only 3 or 4 grains recovered (samples C-41, 42, 45). Previous reports are those of Hammen and Gonzalez (1960) from the Pleistocene-Holocene of Colombia; Tsukada (1966) from core samples of Lake Petenxil, Guatemala, absolute date ( $C^{14}$ ) 4,000 years before present; and Heusser (1966) from Late Pleistocene deposits in the Province of Llanquihue, southern Chile. The genus is also present in our samples from the Miocene Paraje Solo Formation of Veracruz, Mexico. Specimens of fossil wood and leaves of *Podocarpus* have been reported from the lowermost Miocene of Argentina (Berry, 1938), the Late Tertiary of Bolivia (Berry, 1939: 33), and the Eocene of western Tennessee (Dilcher, 1969). An account of the distribution of Podocarpaceae in Southern Hemisphere Cretaceous and Tertiary beds is given by Couper (1953).

*Abutilon* (Fig. 20)

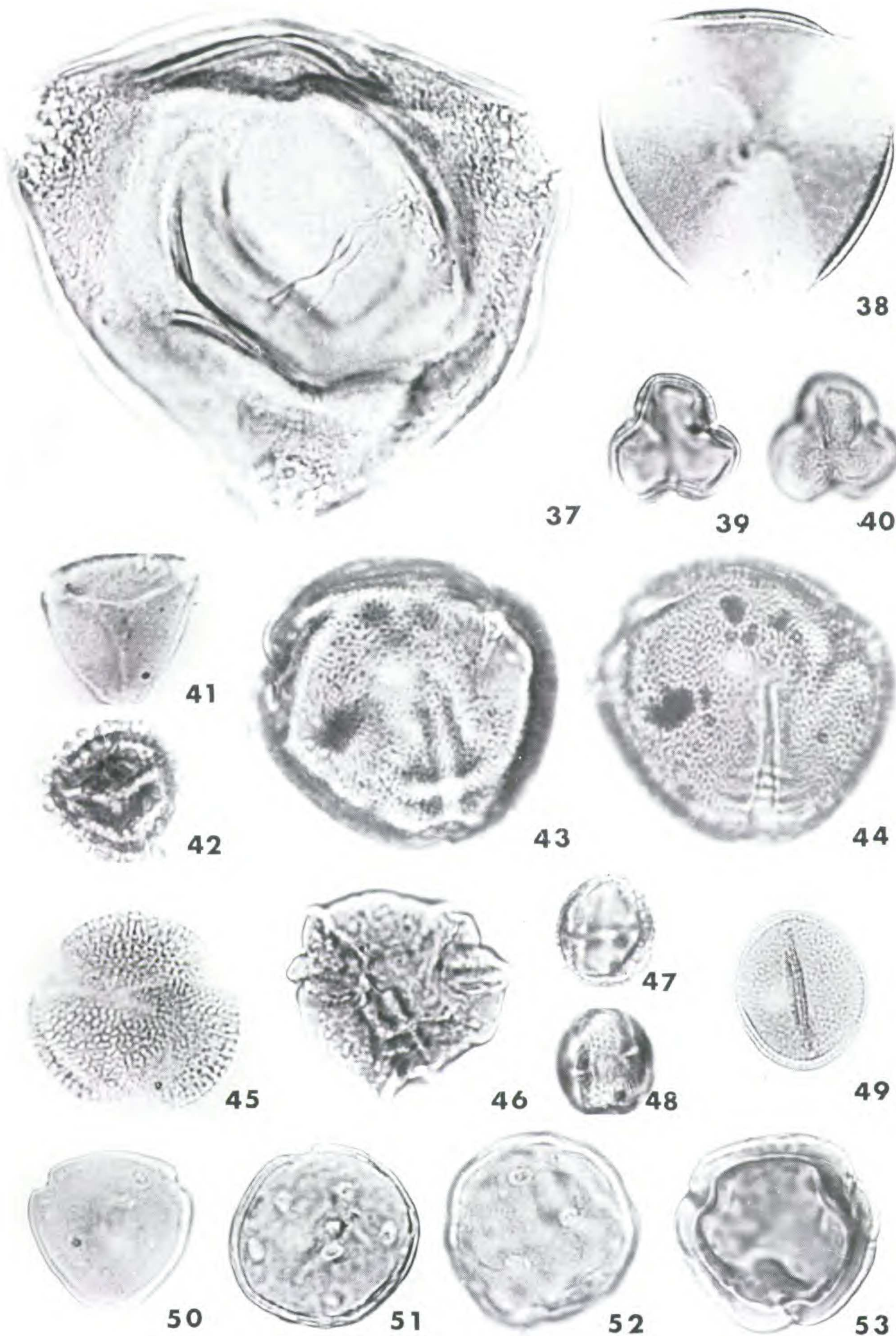
The tropical to warm-temperate genus *Abutilon* (Malvaceae) consists of about 100 species of herbs and shrubs, widely distributed around the world. About 20 species occur in the Antilles with 4–5 in Puerto Rico. Species of *Abutilon* are adapted to a wide range of ecological conditions, including dry rocky slopes, stream-sides, open plains, and more tropical shaded forest conditions. A single grain of *Abutilon* was recovered from sample A-1.

The fossil pollen is very similar to that of the modern *A. incanum*. This species is not found in Puerto Rico today, but grows in western Arizona, Texas, and southward into Baja California, Nuevo León, San Luis Potosí, and Sinaloa, Mexico, on dry rocky slopes (Shreve & Wiggins, 1964: 880). This distribution



FIGURES 16–36.—San Sebastian (Oligocene) microfossils, Puerto Rico. — 16. *Podocarpus*,  $40 \times 68\mu$  (C-41,7; ESF U-37, 1–2). — 17. *Aetanthus*  $32\mu$  (C-46,1; ESF H-41,3). — 18, 35–36. *Alchornea*,  $22\mu$  (C-45,10; ESF G-46,4). — 19. *Brunellia*,  $24\mu$  (C-42,15; ESF U-31,1). — 20. *Abutilon*,  $45\mu$  (A-1,1; ESF H-36,1–2). — 21. *Faramea*,  $32\mu$  (C-46,6; ESF T-44,3). — 22. *Bombax*,  $43\mu$  (B-14; ESF O-17,2). — 23. *Bursera*,  $29\mu$  (B-17,5; ESF V-16,2). — 24–25. *Catostemma*,  $33\mu$  (C-43,1; ESF K-39,2). — 24. Outline.—25. Surface.— 26. *Casearia*,  $18 \times 23\mu$  (C-42,15; ESF S-36,4). — 27. *Chrysophyllum*,  $13.5 \times 18.9\mu$  (C-41,1; ESF K-33,4). — 28–29. *Corynostylis*,  $25\mu$  (C-47,1; ESF P-22,2–4).—28. Outline.—29. Surface. — 30–31. *Dendropanax*,  $25\mu$  (C-46,15; ESF J-20,4).—30. Outline.—31. Surface. — 32. *Guarea*,  $36\mu$  (C-43,2; ESF U-42,1). — 33–34. *Fagus*,  $39\mu$  (A-1,1; ESF D-32,1).







pattern is somewhat different from other living counterparts of the microfossils, but there is some megafossil evidence that *A. incanum* may have had a wider distribution in the past. Hollick (1928) described fossil fruits from the Collazo Shales of Puerto Rico as *Malvocarpon clarum*. He states that “. . . generic relationship with *Abutilon* is strongly indicated by the shape and arrangement of the carpels” (p. 214) and compares the specimens to fruits of the modern *A. texense*, a synonym of *A. incanum* (*vide* Shreve & Wiggins, 1964: 880). Other reports of megafossils of *Abutilon* are Hollick (1936) from the Paleocene or Eocene of Alaska, and Berry (1925: 217), who described *Malvacarpus tertarius* from Miocene deposits in Argentina and compared it to several modern genera including *Abutilon*.

#### *Acacia* (Fig. 14)

*Acacia* includes some 700 species distributed in warm-temperate regions; the largest concentrations are in Africa and Australia. The number of native species in regions with which the fossil assemblage has affinities is relatively few (*e.g.*, 1 species in Cuba, 17 species in northern Mexico; *vide* Shreve & Wiggins, 1964). The pollen of 60 species, including most of those from Latin America, were compared with the microfossils. The fossil is characterized by its exceptional size ( $72\mu$ ) and scabrate exine. These features are not common in modern species of *Acacia*, but are characteristic of *A. farnesiana*. This plant is a spiny shrub or small tree (3–4 m tall) of thickets and forests in the dry coastal limestone regions of Puerto Rico. Its geographic range is throughout Latin America and into southern Texas, California, and Arizona, and through cultivation along the Gulf States to Florida. It is considered to be introduced in the Antilles, although there is some debate about its natural occurrence in Cuba. The presence of *A. farnesiana* pollen in the San Sebastian microflora suggests it may be native to Cuba and other islands of the West Indies. Tsukada (1966) found *Acacia* polyads in Recent deposits from Guatemala, and Heusser (1966) reported *Acacia* from Late Pleistocene deposits in southern Chile. Megafossils identified as *Acacia* also occur in the Pliocene floras of Potosí, Bolivia (Berry, 1939: 45).

#### *Aetanthus* (Fig. 17)

The genus *Aetanthus* (Loranthaceae) is presently restricted to the northern Andes. There are about 15 species which grow in temperate forests at elevations of about 2,000 m. A single specimen was recovered from sample C-46. The genus has not previously been reported from the fossil record.



FIGURES 37–53.—San Sebastian (Oligocene) microfossils, Puerto Rico. — 37. *Hauya*,  $85\mu$  (C-42,9; ESF P-23,2). — 38. *Jacaranda*,  $50\mu$  (C-46,8; ESF J-37,2). — 39–40. *Marcgravia*,  $19\mu$  (C-42,15; ESF R-29,4). — 39. Outline. — 40. Surface. — 41. *Eugenia*,  $27\mu$  (C-45,3; ESF L-19). — 42. *Ilex*,  $25\mu$  (C-47,15; ESF H-19). — 43–44. *Nyssa*,  $50\mu$  (C-41,1; ESF D-37,4). — 43. Outline. — 44. Surface. — 45. *Oxalis*,  $32\mu$  (A-12,1; ESF P-32,1). — 46. *Rauwolfia*,  $35\mu$  (B-39,1; ESF C-45,4). — 47–48. *Zanthoxylum*,  $13 \times 18\mu$  (C-50,15; ESF N-26). — 47. Outline. — 48. Surface. — 49. *Pleodendron*,  $23\mu$  (C-41,6; ESF E-24,4). — 50. *Engelhardia*,  $27\mu$  (C-44,1; ESF U-24,3). — 51–52. *Liquidambar*,  $35\mu$  (C-43,1; ESF V-37,3). — 51. Outline. — 52. Surface. — 53. *Norantea*,  $33\mu$  (C-50,15; ESF N-30,4).



*Alchornea* (Fig. 18, 35–36)

Members of the genus *Alchornea* (Euphorbiaceae) are pantropical. There are about 70 widely distributed species (Fig. 71), represented in the New World tropics by a well-circumscribed section, *Alchornea*. Forty species occur in South America where they are common members of hydrosere successions along river banks and swamps. Species from Mexico and Central America are fewer in number and commonly grow in rain forests, wet lowlands, and rocky montane areas.

A single species, *A. latifolia*, grows in Puerto Rico today (Little & Wadsworth, 1964: 262). It is a medium-sized, rapid-growing evergreen tree attaining heights of 10–20 m. The trees are most common in the montane rain forests (e.g., Cerro de Punta), but they also occur in moist limestone coastal regions, growing mainly in openings and along roadsides. This species also occurs on Cuba, Jamaica, Haiti (*A. haitiensis* also present), and Tortola; and from Veracruz, Mexico, south to western Panama (G. L. Webster, personal communication, 1969).

Microfossils of *Alchornea* are common in the San Sebastian Formation, occurring in nearly every sample (0.5–1.0%). They also occur in Pleistocene deposits from El Salvador and Guatemala (Tsukada & Deevey, 1967), Upper Cretaceous-Tertiary of Guyana (Hammen & Wijmstra, 1964, as *Psilatricolporites operculatus*), in the Lower and Middle Eocene of Tibu, Colombia (Gonzalez-Guzman, 1967), and in our Miocene samples from the Paraje Solo Formation, Veracruz, Mexico.

*Bernoullia* (Fig. 15)

There are two species of *Bernoullia* (Bombacaceae) distributed from southern Mexico through Central America into the tropical regions of northern South America (Fig. 72). These are large trees (30 m tall) and are deciduous during the latter part of the dry season. Microfossils are common at Locality C with an abundance as high as 2.5%. There are no other reports of the genus in the fossil record.

*Bombax* (Fig. 22)

Members of *Bombax* are tropical and include about eight species in Mexico, Central and South America. The plants are common in damp tropical forests.

Microfossils of *Bombax* are rare in the Puerto Rican samples, with a single specimen recovered from Locality B-14 and B-24. Previous reports include Hammen (1954, as *Bombacacidites annae*) from the Lower Tertiary of Colombia, Norem (1955) from the Eocene of Venezuela, and Hammen (1963) from Quaternary deposits in Guyana. Tsukada (1966) also reports *Bombax* from Recent core material of Lake Petenxil, Guatemala.

*Brunellia* (Fig. 19)

The genus *Brunellia* (Brunelliaceae) consist of 45 species distributed in the Neotropics from Mexico through Central America to Peru. It is represented in Puerto Rico by *B. comocladifolia*, a medium-size evergreen tree (5–10 m tall) of the montane forests to elevations of 1,500 m or higher (Little & Wadsworth,



1964). The range of *B. comocladifolia* is throughout the Greater Antilles, Guadeloupe, and Venezuela and Colombia.

Microfossils were recovered from samples C-43 and C-48 (1.0–1.5%). The fossils are similar to several modern species of *Brunellia*, including *B. comocladifolia*. The genus has not previously been reported from the fossil record.

#### *Bursera* (Fig. 23)

The genus *Bursera* (Burseraceae) is warm-temperate to tropical in distribution, consists of about 100 species, and occurs throughout Mexico, Central America, the Antilles, and northern South America (Brizicky, 1962a). The western Mexican species have recently been monographed by McVaugh and Rzedowski (1965). The most widespread species is probably *B. simaruba* which grows through the entire range of the genus (Little & Wadsworth, 1964). In Puerto Rico this species is a medium-size deciduous tree 20–40 feet tall and is common in deciduous forests with soils derived from limestone.

A single pollen grain was recovered from sample B-17. It is similar to a number of modern species including *B. simaruba*. Pollen of *Bursera* is also known from Recent core sediments from Lake Petenxil in northern Guatemala, Tsukada, 1966). Megafossils of *Bursera* are reported from the Lower Oligocene Florissant beds of Colorado (MacGinitie, 1953; cf. McVaugh & Rzedowski, 1965: 318).

#### *Casearia* (Fig. 26)

*Casearia* (Flacourtiaceae), with about 160 species, is pantropical in distribution. Some 40 species occur in Mexico and Central America; 90–100 grow in South America and about 25 in the West Indies (Fig. 73). At least seven species are native to Puerto Rico; *C. arborea*, *C. aculeata*, *C. bicolor*, *C. decandra*, *C. guianensis*, *C. ramiflora*, and *C. sylvestris*. In Puerto Rico the genus is widely distributed along roadsides, thickets, and in the lower montane moist limestone and moist coastal regions. It is a small evergreen tree (10 m tall), which invades the understory of moist tropical forests.

Pollen of *Casearia* occurs only in samples C-42 and C-47, with an abundance of less than 0.5%. Hammen and Wijmstra (1964) illustrate pollen similar to *Casearia* from the Tertiary of Guyana as *Psilatricolporites cyamus*. Berry (1938: 106–107) reported leaf material from the Lower Miocene of Río Pichileufu, Argentina, as similar to the modern *C. arguta*. In the same paper Berry states that the only previous report was that of Engelhardt from the Lower Miocene of Chile.

#### *Catostemma* (Fig. 24–25)

The genus *Catostemma* (Bombacaceae) is a New World group of six species distributed in Guyana, Venezuela, and Brazil. The trees are most abundant in the tropical rainforests of Guyana where the average annual rainfall is over 250 cm. Here they reach heights of 30 m and are codominants in the canopy layer along with *Mora* and *Eschweilera* (Richards, 1966: 238–239).

Pollen of the six species of *Catostemma* can be separated into two groups. One type (four species) is 4–6 stephanocolpate with a densely and evenly perforated tectum. The second type is 4–6 stephanoporate and echinate; *C. praecox*



and *C. micranthum* are included here. The microfossils are of the latter type. Presently *C. praecox* and *C. micranthum* are restricted to the rain forests of Brazil.

The abundance of *Catostemma* pollen in the San Sebastian Formation is 0.5% in sample A-12, and it is common at Locality C. Pollen has also been reported from the Upper Eocene to earliest Oligocene of Guyana and is cited as occurring into the Lower Miocene of the Caribbean area (Germeraad, *et al.*, 1968). According to these authors the pollen shows strong local abundance especially in the Oligocene and Lower Miocene. Other reports of fossil pollen of *Catostemma* are those of Hammen (1963) from the Quaternary of Guyana and probably that of Norem (1955) from the Upper Eocene of Venezuela, listed as "tetracolpate pollen." The presence of *Catostemma* pollen in the Puerto Rican samples considerably extends the known geographic range of the genus during Tertiary times.

#### *Chrysophyllum* (Fig. 27)

This large genus of Sapotaceae is distributed throughout the tropical regions of the world. It is especially common in the American tropics (Fig. 74). Species in the New World are found in the moist wooded and montane forests of Mexico, Central America, and throughout the West Indies; one species, *C. oliviforme* occurs in southern Florida (Wood & Channell, 1960).

Three species are common to Puerto Rico and adjacent islands—*C. argenteum*, *C. cainito*, and *C. oliviforme*. These are evergreen shrubs or trees reaching heights up to 15 m (Little & Wadsworth, 1964). The trees are common in the moist limestone and lower montane forests, primarily in northern and western Puerto Rico.

Microfossils of *Chrysophyllum* are present in samples B-25 (0.5%) and C-41 and C-47 as single specimens. The pollen of *Chrysophyllum* is similar to some members of the Burseraceae, although pollen of the Burseraceae is usually about 50% larger. Hollick (1928) described two species and one variety of megafossils of *Chrysophyllum* from the Collazo River area. He compared this material to *C. argenteum* and *C. cainito*. Other reports of megafossils are Berry (1939: 154) from the Pliocene of Venezuela, and Berry (1938: 45) from the Eocene of Venezuela.

#### *Corynostylis* (Fig. 28–29)

The genus *Corynostylis* (Violaceae) consists of only four species, distributed from Veracruz, Mexico, into South America (Fig. 75). The most wide-ranging species, *C. arborea*, is a woody vine reaching tree girth. It is common along river banks in tropical forests. This species grows throughout the range of the genus, while the others are restricted to Brazil, Colombia, and Peru.

Microfossils of *Corynostylis* occur in samples B-19, C-43, C-47, and C-50 with an abundance of 0.5%. There are no other reports of *Corynostylis* in the fossil record.

#### *Dendropanax* (Fig. 30–31)

The genus *Dendropanax* (Araliaceae) occurs in tropical and subtropical regions throughout the world and includes about 75 species. The American species (about 45) occur in Mexico as far north as the state of Tamaulipas, throughout



Central America, and into South America (Fig. 76). *Dendropanax* is common in montane forests and mainly consists of trees with a few shrubs. A medium-size evergreen tree reaching heights of 15 m or more, *D. arboreus* is common in Puerto Rico. It grows in the lower montane and moist limestone regions of Puerto Rico and is common in the coffee plantations of the Central and Western Cordilleras. Another species, *D. laurifolia*, also grows in Puerto Rico but is not as common.

The fossil pollen is rare, being recovered only from sample C-48 (0.5%). The only other fossil record of *Dendropanax* is by Dilcher and Dolph (1970), who reported leaves in Eocene deposits of western Tennessee.

#### *Engelhardia* (Fig. 50)

At present there are four species recognized in *Engelhardia*—*E. pterocarya* from Costa Rica; *E. mexicana* from Mexico, Guatemala, and Costa Rica; *E. nicaraguensis* from Nicaragua; and *E. guatemalensis* from Guatemala. According to D. E. Stone these can be reduced to two, *E. pterocarya* and *E. mexicana*, the latter with three subspecies (*cf.* also Manning, 1959). The genus has a discontinuous distribution along the cordillera from Orizaba, Mexico, to Boquete, Panama, and one collection is known from Colombia. *Engelhardia* is not known from the West Indies. These medium-size trees commonly grow at elevations of 1,000–1,500 m in wet mountains.

Fossil pollen of *Engelhardia* occurs at all localities, and at Locality C it constitutes 30–50% of the samples. Other reports include those of Traverse (1955) from the Oligocene (?) Brandon Lignite of Vermont; Wodehouse (1933) from the Eocene Green River Formation of Colorado and Utah; and Langenheim *et al.* (1968) from Oligo-Miocene deposits in Chiapas, Mexico. It is common in the Paraje Solo (Miocene) Formation of Veracruz, Mexico. Pollen of the genus is also recorded in several presently unpublished theses and manuscripts on Mississippi Embayment and British Columbia deposits. If all these reports are valid, *Engelhardia* formerly had an extensive geographic range and probably broader ecological tolerances. Reported megafossils are common in Tertiary deposits of the western United States (LaMotte, 1952).

#### *Eugenia* (Fig. 41)

The genus *Eugenia* (Myrtaceae) contains several hundred species—500 according to Wilson (1960). McVaugh (1963) states that as many as 2500 names have been referred to *Eugenia*. It is widely distributed throughout tropical and subtropical regions. About 150 species occur in Mexico and Central America, and at least 135 are found in South America, concentrated in Brazil. Eighty or more are reported from the West Indies, and at least 25 are found in Puerto Rico (Fig. 77; Little & Wadsworth, 1964). Among the common species are *E. aeruginea*, *E. rhombea*, and *E. stahlii*, which are small, erect evergreen trees (10–20 m tall) found in the montane forests at elevations up to about 1,000 m.

Microfossils of *Eugenia* are recorded from Locality C (0.5%). Other reports are Hammen and Gonzalez (1960) from Pleistocene-Holocene deposits in Colombia, Hammen (1962) from Recent sediments of Laguna de Los Bobos, Colombia, and Tsukada (1966) from Recent core samples of Lake Petenxil, Guatemala.



Megafossils of *Eugenia* have been reported by Hollick (1928) from the Oligocene of Puerto Rico, Berry (1929) from the Loja Basin (Late Miocene) of Ecuador, Berry (1937: 59) from the Uppermost Miocene of Trinidad, and Berry (1939: 126, 151) from the Miocene of Cuba and the Mio-Pliocene of Venezuela.

*Fagus* (Fig. 34–35)

*Fagus*, with about ten species, is mostly north temperate in distribution with one species, *F. mexicana*, reported from Zacualtipan, Hidalgo, Mexico, at an elevation of 1,800 m. An account of the distribution of *Fagus* in Mexico is given by Fox and Sharp (1954).

Fossils are present in sample A-3 with an abundance of 1.0%. Pollen of six species was compared to the microfossil, and it is most similar to *F. americana*.

*Faramea* (Fig. 21)

The genus *Faramea* (Rubiaceae) contains about 180 species of trees and shrubs which are widely distributed in Latin America (Fig. 78). Among these *F. occidentalis* is common in Puerto Rico. It is a shrub or small evergreen tree (3–10 m tall) and is common in the understory of moist limestone and lower montane regions.

The pollen of *Faramea* is dimorphic (Willis, 1966: 444), with 2- and 3-porate grains. The pollen of *F. occidentalis* is typically 3-porate, as is the microfossil. The pollen is present in samples B-25 (1.5%) and C-41 (less than 0.5%). The genus has not previously been reported in the fossil record.

*Guarea* (Fig. 32)

This genus of Meliaceae consists of about 150 species in Latin America (Fig. 79) and some 20 species in Africa. In Puerto Rico they are shrubs (*ca.* 2–3 m tall) to large evergreen trees (15–25 m tall) common in the moist forests of the lower montane limestone and moist coastal regions. Species in Puerto Rico include *G. guara*, *G. humilis*, *G. ramiflora*, and *G. trichilioides*. *Guarea ramiflora* along with *Lucuma multiflora* comprise the Maricao forests. The crown layer of this forest is mainly *G. ramiflora* and the ground cover is primarily seedlings of this species (Gleason & Cook, 1926).

Microfossils were recovered from Localities B and C (0.5%). Hollick (1928) reported *G. opinabilis* from the Oligocene of Puerto Rico, and Hollick and Berry (1924) described leaves of the genus from the Late Tertiary of Brazil and referred them to the modern *G. trichilioides*. Graham (1962*b*) transferred fruits described as *Ficus ceratops* from Upper Cretaceous beds of Wyoming to *Guarea*.

*Hauya* (Fig. 37)

*Hauya* consists of three species, *H. heydeana* (Chiapas, Mexico, and Guatemala), *H. microcerata* (Chiapas south to Honduras and El Salvador), and *H. elegans* (Hidalgo and San Luis Potosí, Mexico, south to Costa Rica). *Hauya glauca* is considered a subspecies of *H. microcerata* (Raven, personal communication, 1969). The pollen of other genera closely related to *Hauya* (*Calylophus*, *Clarkia*, and *Gaura*) was examined and found to be distinct from *Hauya*.



Ecologically *Hauya* occurs with oaks and other lush middle elevation vegetation. It does not range upward into the pine belt or downward into the seasonally drier deciduous vegetation. It is always rare, and phylogenetically is one of the most primitive genera of Onagraceae (Raven, personal communication, 1969).

During the Oligocene *Hauya* had a distribution considerably different than at present, and it grew in the West Indies where it no longer occurs. Microfossils were recovered from Locality C (less than 0.5%); there are no other reports of *Hauya* in the fossil record.

#### *Ilex* (Fig. 42)

The genus *Ilex* is widespread and includes about 400 species. At least 60 grow in Mexico, Central America, and the West Indies; and some 180 species occur in South America. These trees and shrubs occupy a wide variety of habitats from wet, tropical rain forests, pine forests, marshy thickets and swamps to mountain slopes. Four species are known from mountain slopes and wooded valleys of Puerto Rico—*I. macfadyenii*, *I. nitida*, *I. obcordata*, and *I. sintenisii*.

A single specimen was recovered from sample C-47. Previous reports from Latin America are those by Hammen and Gonzalez (1960) from Upper Pleistocene and Holocene deposits near Bogotá, Colombia, Hammen (1962) from Recent sediments (5,000 yrs.) of Laguna de los Bobos, Colombia, Hammen (1963) from the Quaternary of Guyana, and Tsukada (1966) from core material of Lake Petenxil, Guatemala.

#### *Jacaranda* (Fig. 38)

There are about 50 species of *Jacaranda* in Latin America (Fig. 80). The only species in Puerto Rico, *J. mimosifolia*, is introduced from Argentina (Little & Wadsworth, 1964). In its native habitat it is common in wet forests and on wooded hillsides.

The pollen of *Jacaranda* is similar to *Tecoma* (cf. Fig. 38, 58), but the former is considerably larger. The single microfossil is present in sample C-46. There are no other reports of the genus in the fossil record.

#### *Liquidambar* (Fig. 51–52)

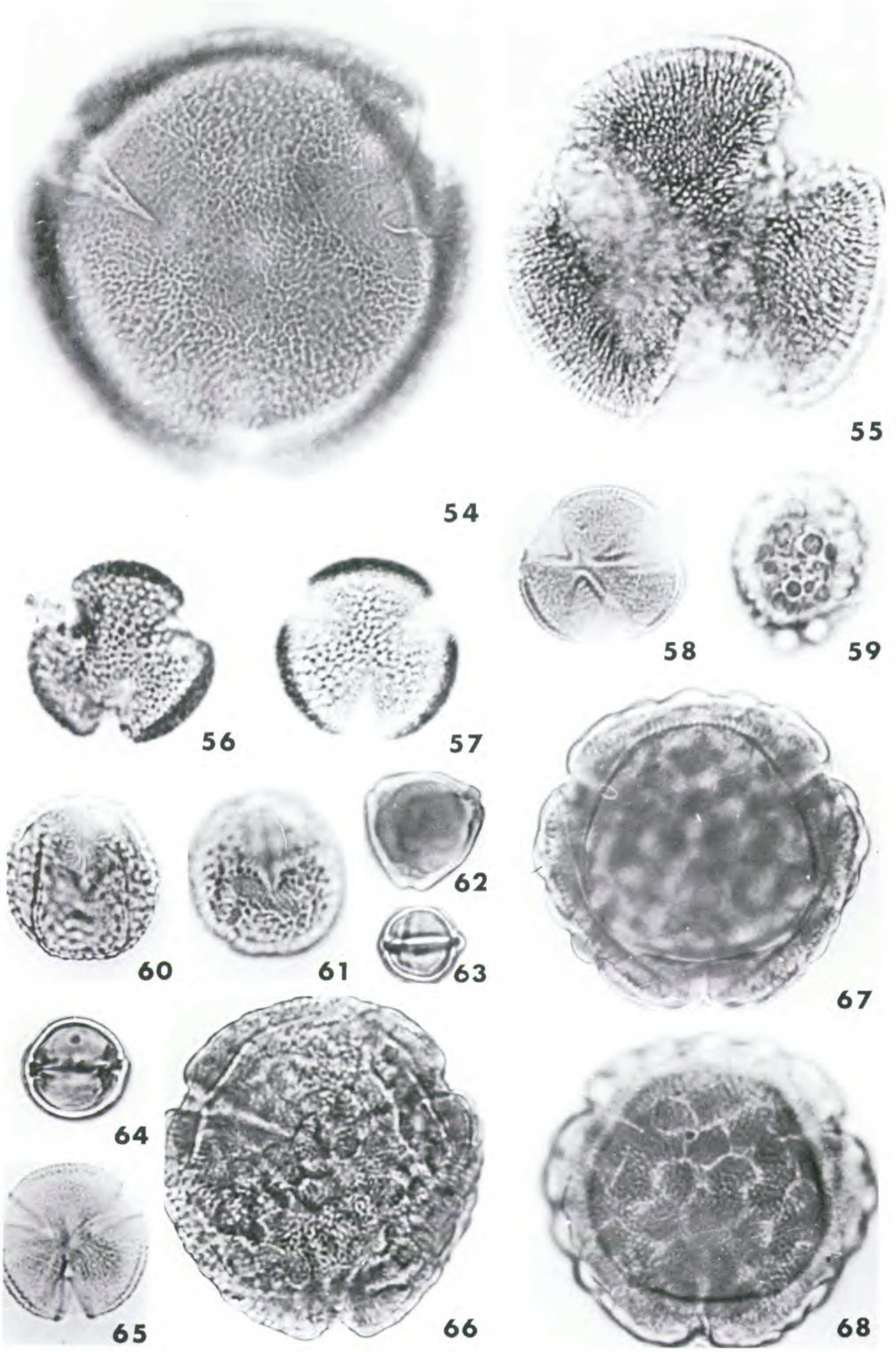
There are three species of *Liquidambar* in the Atlantic States and Eastern Asia (Ernst, 1963). The species from the eastern United States, *L. styraciflua*, is common in deciduous forests along river flood plains and other mesic temperate habitats. It ranges into Mexico and Honduras (as *L. macrophylla* or *L. styraciflua* var. *mexicana*) and grows in the montane forests at elevations of 1,000–2,000 m.

Microfossils of *Liquidambar* are present at Locality C with an abundance of 0.5–2.0%. Tsukada (1966) has reported pollen from Recent core samples, Lake Petenxil, Guatemala. A review of the fossil history of the genus, based on pollen data, is given by Kuprianova (1960). There are numerous reports of megafossils (LaMotte, 1952).

#### *Marcgravia* (Fig. 39–40)

The genus *Marcgravia* (Marcgraviaceae) occurs in Central and South America and the West Indies (Fig. 81). There are about 55 species of these climbing,







epiphytic shrubs, including *M. sintensisii* and *M. rectiflora*. The latter is common in the rain forests of Puerto Rico and under favorable conditions the adult plant, 2–3 m in diameter, becomes a dominant feature of the forest.

A single pollen grain was recovered from sample C-42. Its infrequent occurrence is consistent with the small amount of pollen produced by the cleistogamous flowers of some species. The genus has not previously been reported from the fossil record.

*Merremia* (Fig. 55)

*Merremia* (Convolvulaceae) grows in warm temperate regions throughout the world (Willis, 1966). There are about 80 species, and 40 of these are found in the neotropics (Fig. 82). The plant is a herbaceous liana, commonly an early invader in secondary successions (Richards, 1966: 393). Eight species grow in the West Indies occupying open places, bluffs, and dry lowland habitats (*M. aegyptia*, *M. alata*, *M. cissoides*, *M. dissecta*, *M. quinquefolia*, *M. tridentata*, *M. tuberosa*, and *M. umbellata*).

The single microfossil specimen from sample C-42 was compared to pollen of species presently growing in the Antilles and is most similar to *M. dissecta*. Fossil pollen has also been reported by Gonzalez-Guzman (1967) from the Lower and Middle Eocene of the Tibu region in Colombia.

*Myrica* (Fig. 62)

The genus *Myrica* is almost cosmopolitan in distribution with 35 known species. There are about 17 species of these trees and shrubs widely distributed throughout Mexico, Central America, and the Antilles. An additional 15 or more are known from South America. Two common members of the Puerto Rican flora are *M. deflexa* and *M. splendens*. These are medium-size, evergreen trees (3–10 m tall), growing in the shaded understory of the lower montane forests on nearly all the islands of the Antilles.

A single microfossil was recovered from sample C-42. Previous reports of fossil pollen are those of Hammen and Gonzalez (1960) from the Upper Pleistocene and Holocene of Colombia, Hammen (1962) from Recent sediments (5,000 yrs.) from Laguna de Los Bobos, Colombia, and Tsukada (1966) from Lake Petenxil, Guatemala.

*Norantea* (Fig. 53)

The genus *Norantea* (Marcgraviaceae) includes about 35 species of the American tropics, being most abundant in South America (Fig. 83). They are lianas which superficially resemble *Philodendron* (Willis, 1966: 777).



FIGURES 54–68.—San Sebastian (Oligocene) microfossils, Puerto Rico. — 54, 66–68. *Pelliciera* (C-48,1; ESF D-38,2).—54. 72 $\mu$ .—66. 55 $\mu$ .—67. Outline, 54 $\mu$ .—68. Surface, 54 $\mu$ . — 55. *Merremia*, 63 $\mu$  (C-42,9; ESF P-41,3). — 56–57. *Tetrorchidium*, 32 $\mu$ , (B-14,10; ESF M-22,1).—56. Low focus.—57. High focus. — 58. *Tecoma*, 27 $\mu$  (C-48,1; ESF U-20,4). — 59. *Tournefortia*, 28 $\mu$  (A-12,10; ESF U-34,4). — 60–61. *Salix*, 27 $\mu$  (C-46,15; ESF L-30,3).—60. Outline.—61. Surface. — 62. *Myrica*, 20 $\mu$  (C-42,4; ESF N-43). — 63–65. *Rhizophora* (C-47,1; ESF L-21,3).—63. 14 $\mu$ .—64. 24 $\mu$ .—65. 28 $\mu$ .



A single specimen was recovered from sample C-50. There are no previous reports of *Norantea* from the fossil record.

*Nyssa* (Fig. 43–44)

*Nyssa* (Nyssaceae) consists of about five or six species distributed widely in the Himalayas, eastern Asia, western Malaysia, and eastern North America (Eyde, 1966). The eastern American species, *N. aquatica* and *N. sylvatica*, range from Maine, the Great Lakes, and southern Canada south to the Brazos River in Texas and Lake Okeechobee in Florida. The latter also occurs in the highlands of Hidalgo, Puebla, and Chiapas, Mexico, at elevations of 1,000–1,700 m. It is frequently associated with *Liquidambar*, *Quercus*, and *Pinus strobus*. Miranda (1945) has discussed the presence of *Nyssa* in Mexico.

Microfossils from the San Sebastian Formation are present at Localities A and C and are most common in sample C-48 (4.5%). The fossil record of *Nyssa* is extensive (Eyde, 1963; Eyde & Barghoorn, 1963); however, we know of no other records from northern Latin America.

*Oxalis* (Fig. 45)

The genus *Oxalis* is widely distributed, consisting of about 800 species. It is particularly abundant in Central and South America. At least 20 species grow in the Antilles as small herbs of diverse habitats. Microfossils of *Oxalis* are rare occurring only in sample A-12 (less than 0.5%). There are no previous reports of the genus in Tertiary deposits of Latin America; Brown (1938) has reported *Oxalis* from the Pleistocene of Louisiana, the only other record known to us.

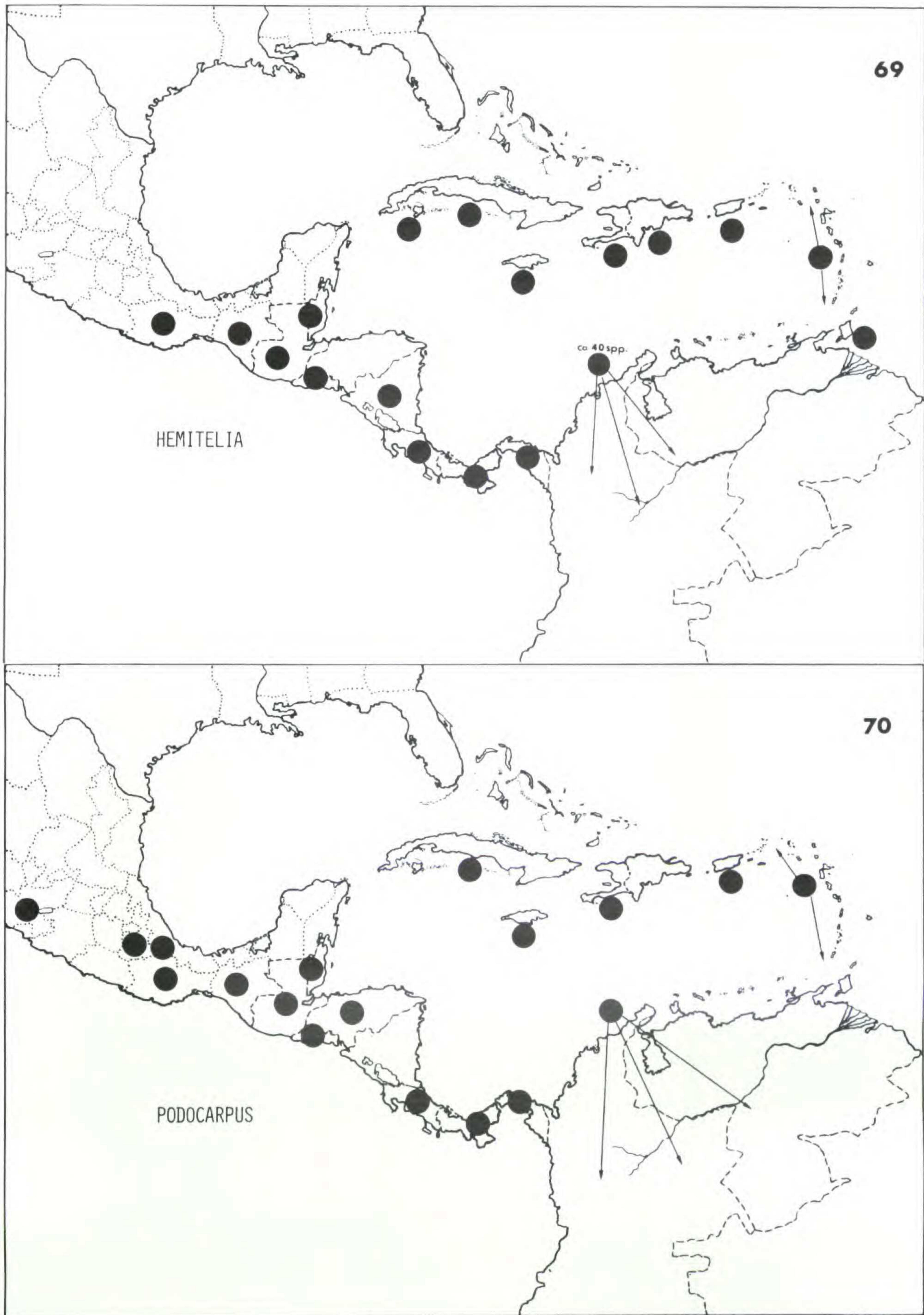
*Pelliciera* (Fig. 54, 66–68)

The genus *Pelliciera* (Theaceae; Pellicieriaceae *vide* Willis, 1966) is represented in the modern flora by a single species, *P. rhizophorae*. It is a small tree, 8–10 m tall, with buttress roots and a mangrove habit. It occurs along sandy beaches, swamps, and mud flats, frequently associated with other mangrove genera. The distribution of *Pelliciera* (Fig. 84) is from Costa Rica, south through Panama, and into northwestern South America (Colombia, Ecuador).

The present range of *Pelliciera* is considerably restricted when compared to its former occurrence. Wijmstra (1968) has reported pollen from Oligocene to Miocene beds of the Guiana Basin of northern South America. Wijmstra also cites references to other occurrences in the Marago Basin of Brazil (Miocene) and from a Miocene pollen flora in Venezuela. Langenheim *et al.* (1967) have identified *Pelliciera* pollen from Oligo-Miocene beds in Chiapas, Mexico. It is also present in our samples of Middle Tertiary age in the Canal Zone, Panama. The fossil record of *Pelliciera* is from the Middle Oligocene to the Present, and these sites are distributed as far north as Chiapas, Mexico and Puerto Rico.

The pollen recovered shows considerable diversity in size and morphology. The grains range in size from 50–90 $\mu$  and include coarsely scabrate to verrucate forms. The same variation is evident in pollen of the modern *P. rhizophorae*.





FIGURES 69-70.—Present Latin American distribution of genera identified from the San Sebastian (Oligocene) Formation, Puerto Rico.—69. *Hemitelia*.—70. *Podocarpus*.



*Pleodendron* (Fig. 49)

The genus *Pleodendron* (Canellaceae) with two species is restricted to the West Indies. *Pleodendron ekmanii* is known only from wooded hillsides in Haiti at elevations of 800 m, and *P. micranthum*, a tall tree of virgin forests, occurs in the Sierra de Luquillo, Puerto Rico, at elevations of about 1,200 m. Microfossils of *Pleodendron* are present in samples C-41, 43, and 50 (0.5%). There are no other fossil records of the genus.

*Rauwolfia* (Fig. 46)

*Rauwolfia* (Apocynaceae) consists of about 100 species distributed throughout tropical regions of the world. There are 15–20 species in Mexico and Central America, about 40 species in South America, and 10–15 from the Antilles. In Puerto Rico the genus is represented by *R. nitida*, a small tree or shrub (7–14 m tall), and *R. viridius*, a shrub about 1–4 m tall (Fig. 85). The plants grow in the coastal and limestone forests and thickets, usually in open habitats.

A single specimen was recovered from sample B-39. There are no other fossil records.

*Rhizophora* (Fig. 63–65)

The genus *Rhizophora* contains 6–9 species distributed throughout the world along tropical coasts. The plants are gregarious trees or shrubs inhabiting mud flats of coastal tidal marshes, brackish streams and lagoons (S. Graham, 1964). Two species grow in areas with which the microflora has affinities—*R. racemosa*, infrequent in the Americas but more common along the African shore, and *R. mangle* which ranges from southern Florida to northern South America.

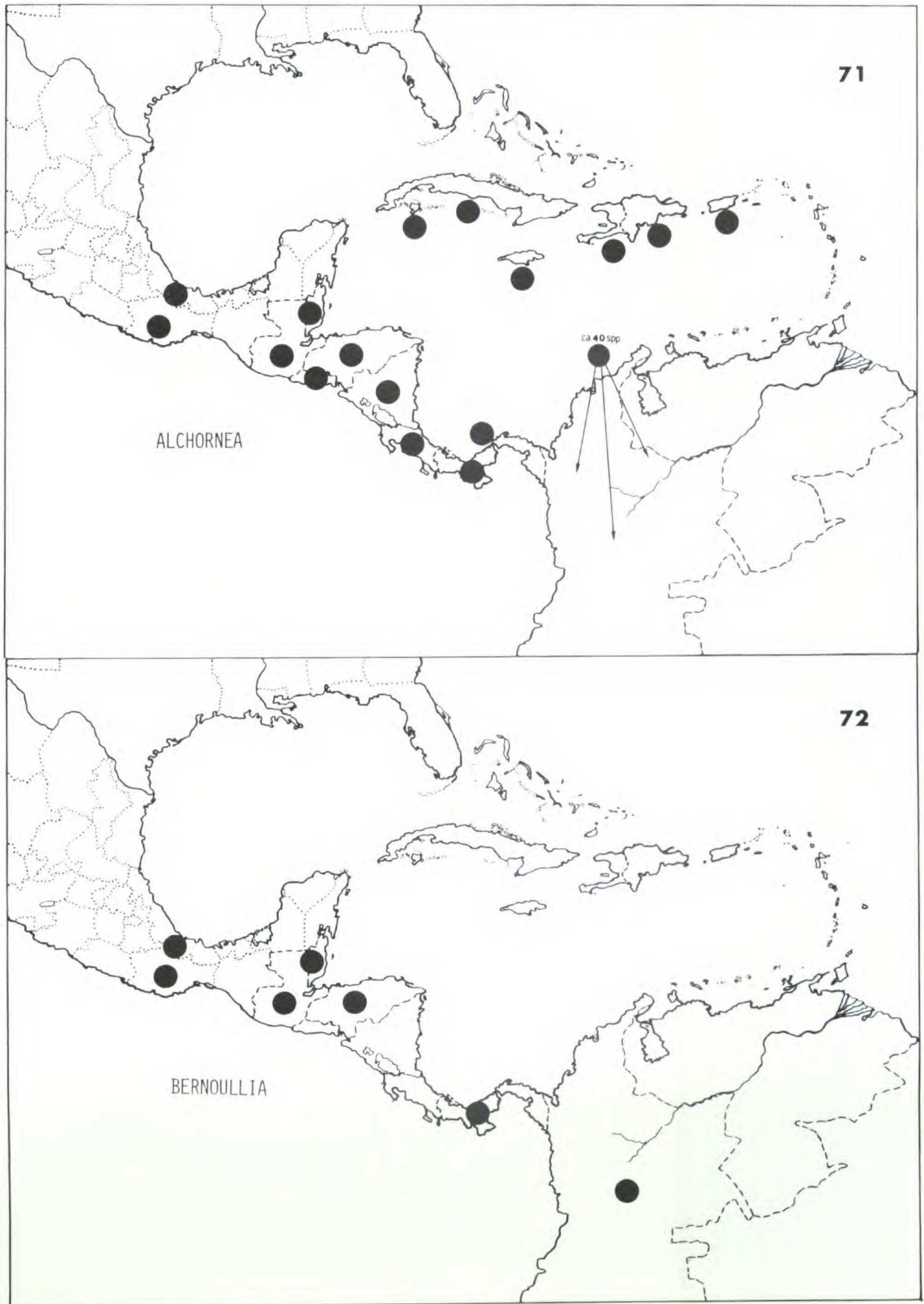
The pollen recovered includes as extremes a small, psilate type with distinct colpi transversales and a larger form with a scabrate surface pattern and less distinct colpi transversales. According to Langenheim *et al.* (1967) these variations are included within the pollen of *R. mangle*.

Fossil pollen of *Rhizophora* is found at all localities with an abundance of 96% at Locality A, 77% at Locality B, and 1–2% at Locality C. Latin American records of the genus are common and include those of Hammen (1963) from the Quaternary of Guayana and Langenheim *et al.* (1967) from the Oligo-Miocene of Chiapas, Mexico. It is also present in our samples from the Miocene of Veracruz, Mexico, and the Middle Tertiary (Oligo-Miocene to Middle Miocene) of Panama. Hollick (1928) records megafossils from the Oligocene of Puerto Rico.

*Salix* (Fig. 60–61)

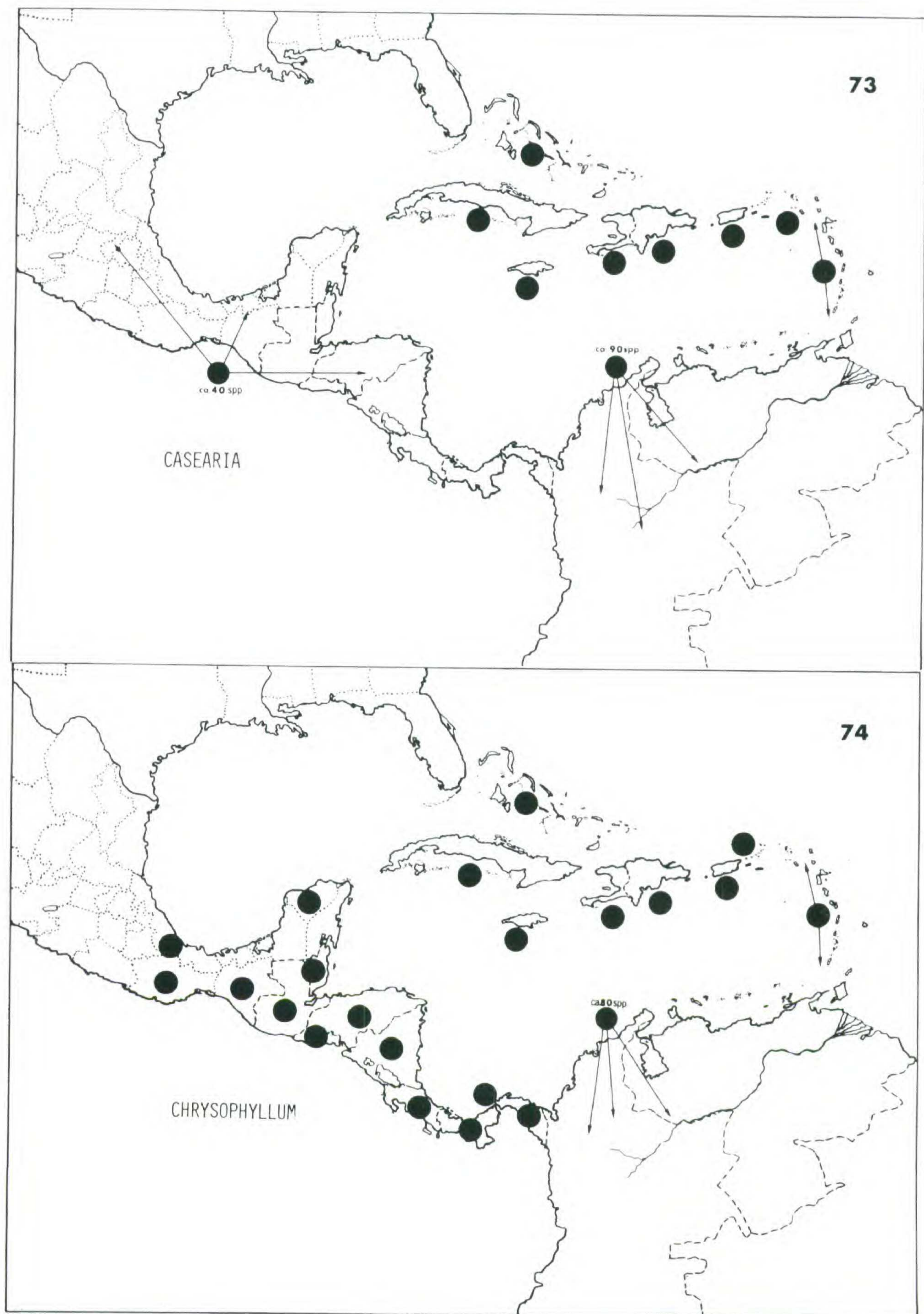
The genus *Salix* includes about 500 species, chiefly north temperate in distribution, but with at least 15 species occurring in Mexico, Central America, and the Antilles. An additional ten species are known from South America. Species of *Salix* range from trees to shrubs and subshrubs, and although most common in moist, mesic environments, they occupy a wide range of habitats. Microfossils were recovered from samples C-43 (1%), C-46 (0.5%), and C-48 (0.5%). We know of no other reports of the genus from Latin American deposits.





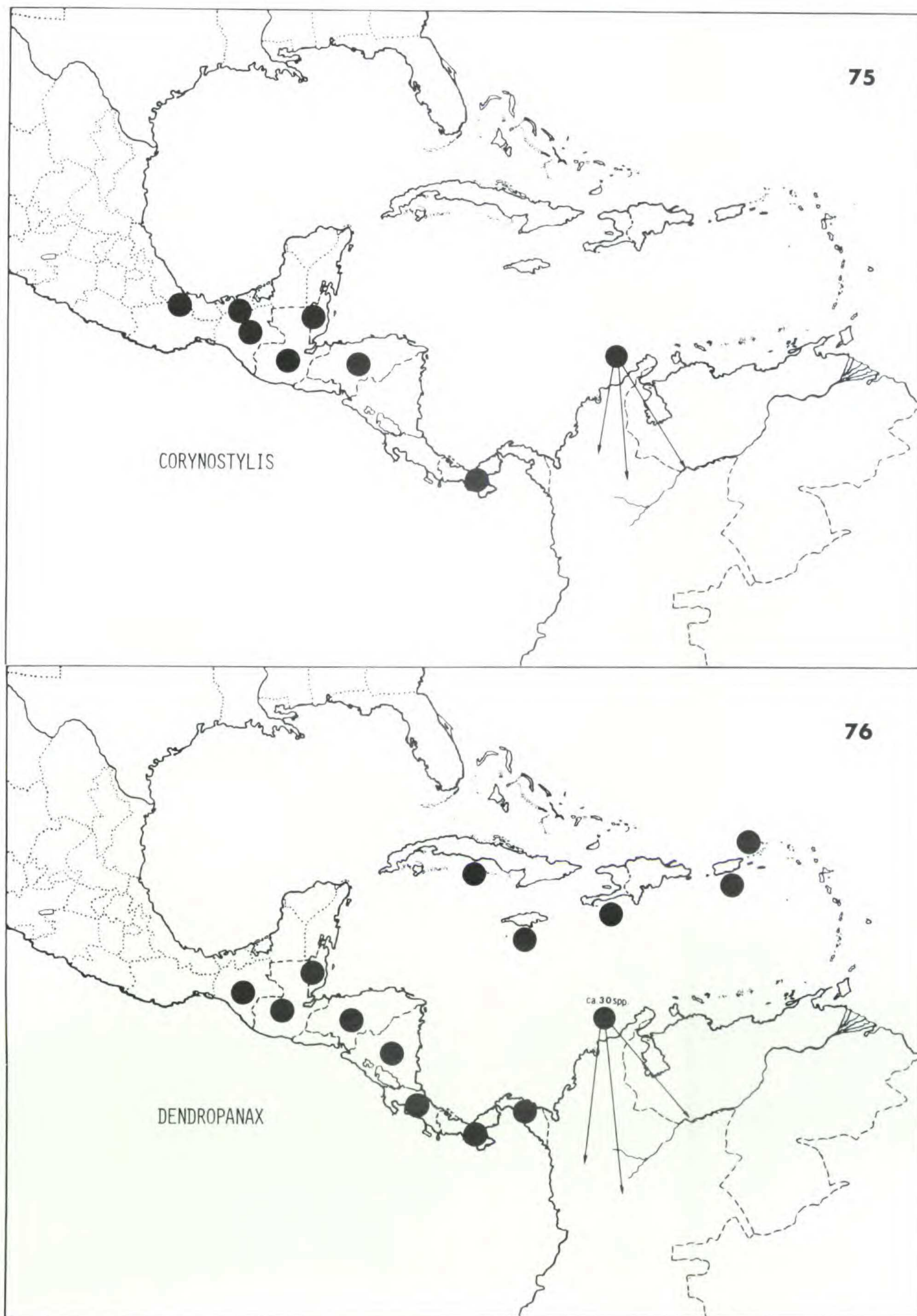
FIGURES 71-72.—Present Latin American distribution of genera identified from the San Sebastian (Oligocene) Formation, Puerto Rico.—71. *Alchornea*.—72. *Bernoullia*.





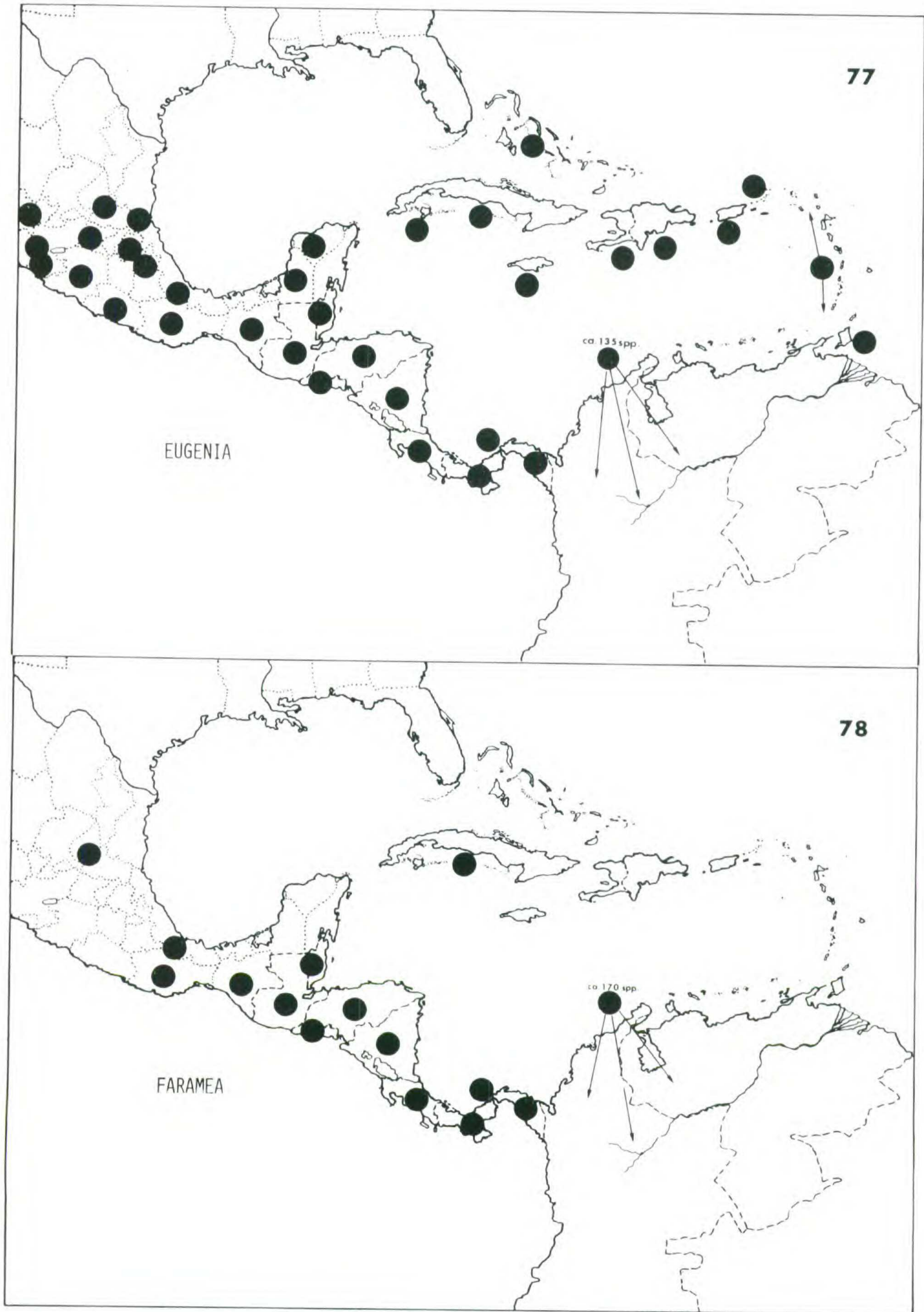
FIGURES 73-74.—Present Latin American distribution of genera identified from the San Sebastian (Oligocene) Formation, Puerto Rico.—73. *Casearia*.—74. *Chrysophyllum*.





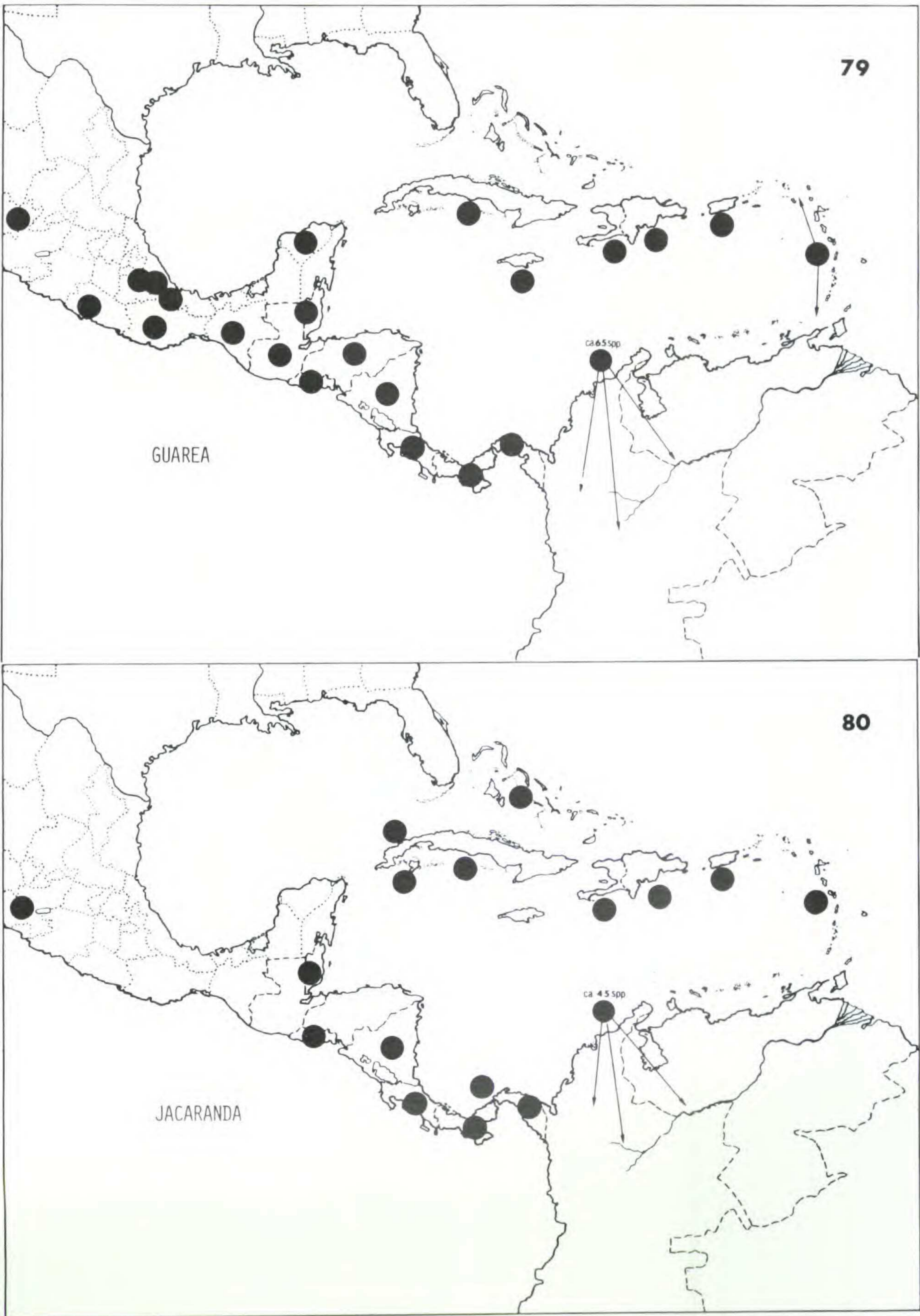
FIGURES 75-76.—Present Latin American distribution of genera identified from the San Sebastian (Oligocene) Formation, Puerto Rico.—75. *Corynostylis*.—76. *Dendropanax*.





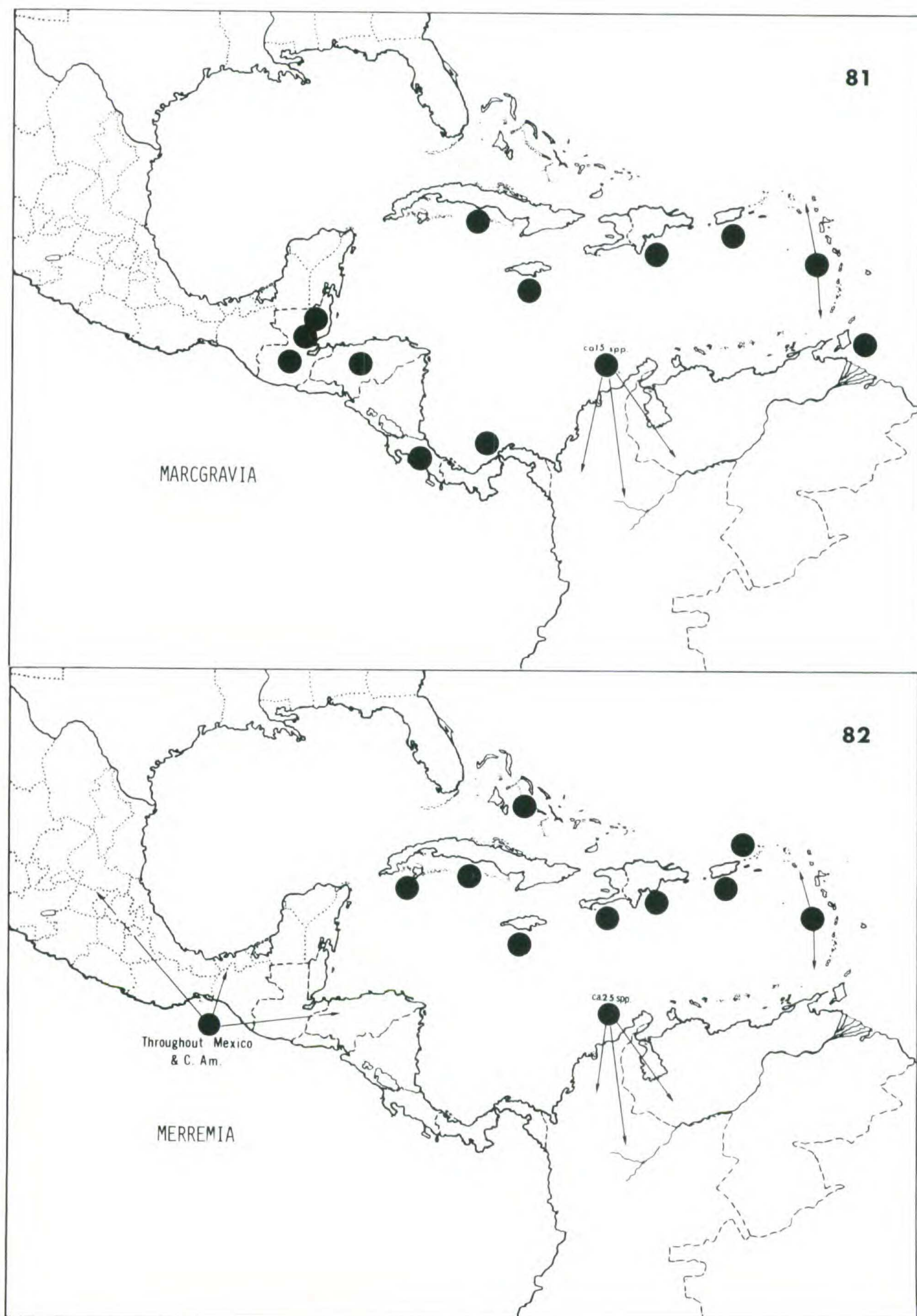
FIGURES 77-78.—Present Latin American distribution of genera identified from the San Sebastian (Oligocene) Formation, Puerto Rico.—77. *Eugenia*.—78. *Faramea*.





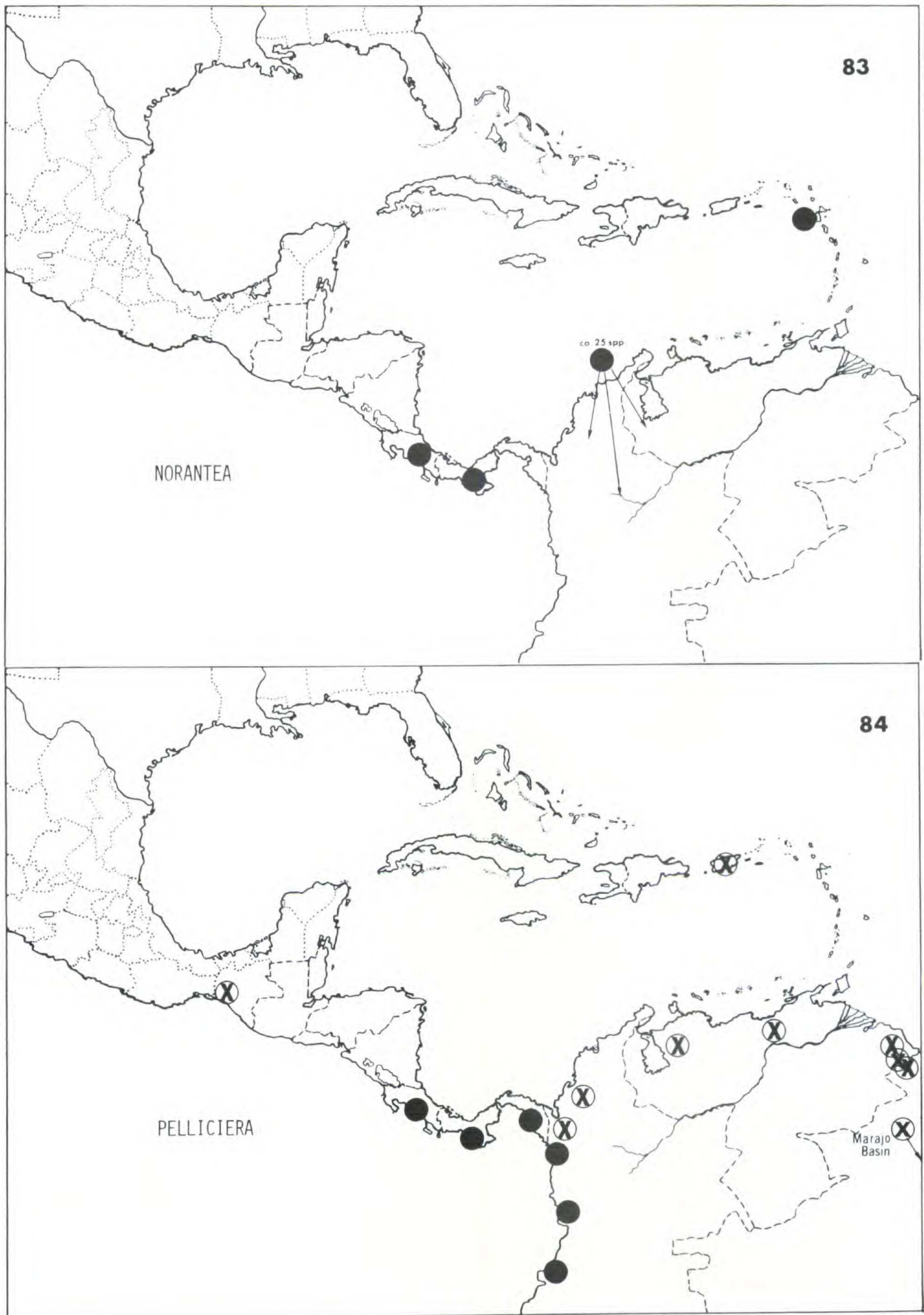
FIGURES 79-80.—Present Latin America distribution of genera identified from the San Sebastian (Oligocene) Formation, Puerto Rico.—79. *Guarea*.—80. *Jacaranda*.





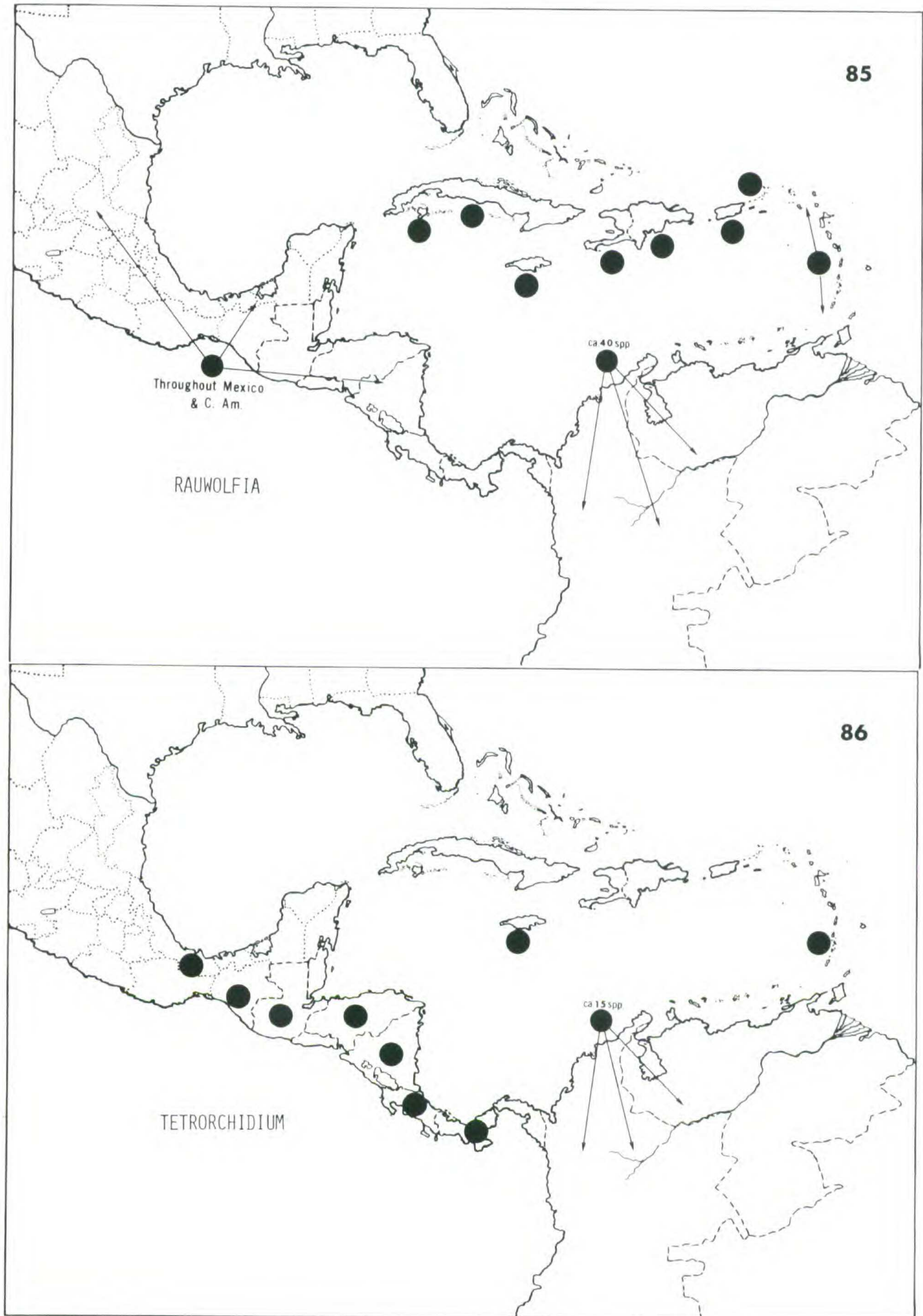
FIGURES 81-82.—Present Latin American distribution of genera identified from the San Sebastian (Oligocene) Formation, Puerto Rico.—81. *Marcgravia*.—82. *Merremia*.





FIGURES 83-84.—Present Latin American distribution of genera identified from the San Sebastian (Oligocene) Formation, Puerto Rico.—83. *Norantea*.—84. *Pelliciera*.





FIGURES 85–86.—Present Latin American distribution of genera identified from the San Sebastian (Oligocene) Formation, Puerto Rico.—85. *Rauwolfia*.—86. *Tetrorchidium*.



*Tecoma* (Fig. 58)

*Tecoma* (Bignoniaceae) ranges from Florida to Mexico, Argentina, and the West Indies. There are about 16 species and one, *T. stans*, is native to Puerto Rico. This species is a small evergreen tree (ca. 8 m tall) and has an extensive geographic range. Pollen of *Tecoma* is rare, occurring only at Locality C (0.5%). There are no other fossil records.

*Tetrorchidium* (Fig. 56–57)

The genus *Tetrorchidium* (Euphorbiaceae) consists of 16 species distributed in Central and South America, the West Indies (but not Puerto Rico), and tropical west Africa (Fig. 86). Gomez-Pompa has recently found the genus in the San Andres Tuxtla area of Veracruz, Mexico (Webster, personal communication, 1969). The plants commonly grow at the upper limits of the montane rain forest. Microfossils are present at all localities and are most frequent at Locality C (1–3%). There are no other fossil records.

*Tournefortia* (Fig. 59)

This genus of Boraginaceae is a tropical to subtropical assemblage of about 150 species. At least 130 are known from the New World, and a number occur on the islands of the West Indies (Fig. 87). These small trees and shrubs are common along moist coastal regions where they are often an important feature of primary succession (Richards, 1966). Microfossils were present only in sample A-12 and were rare. There are no other fossil records.

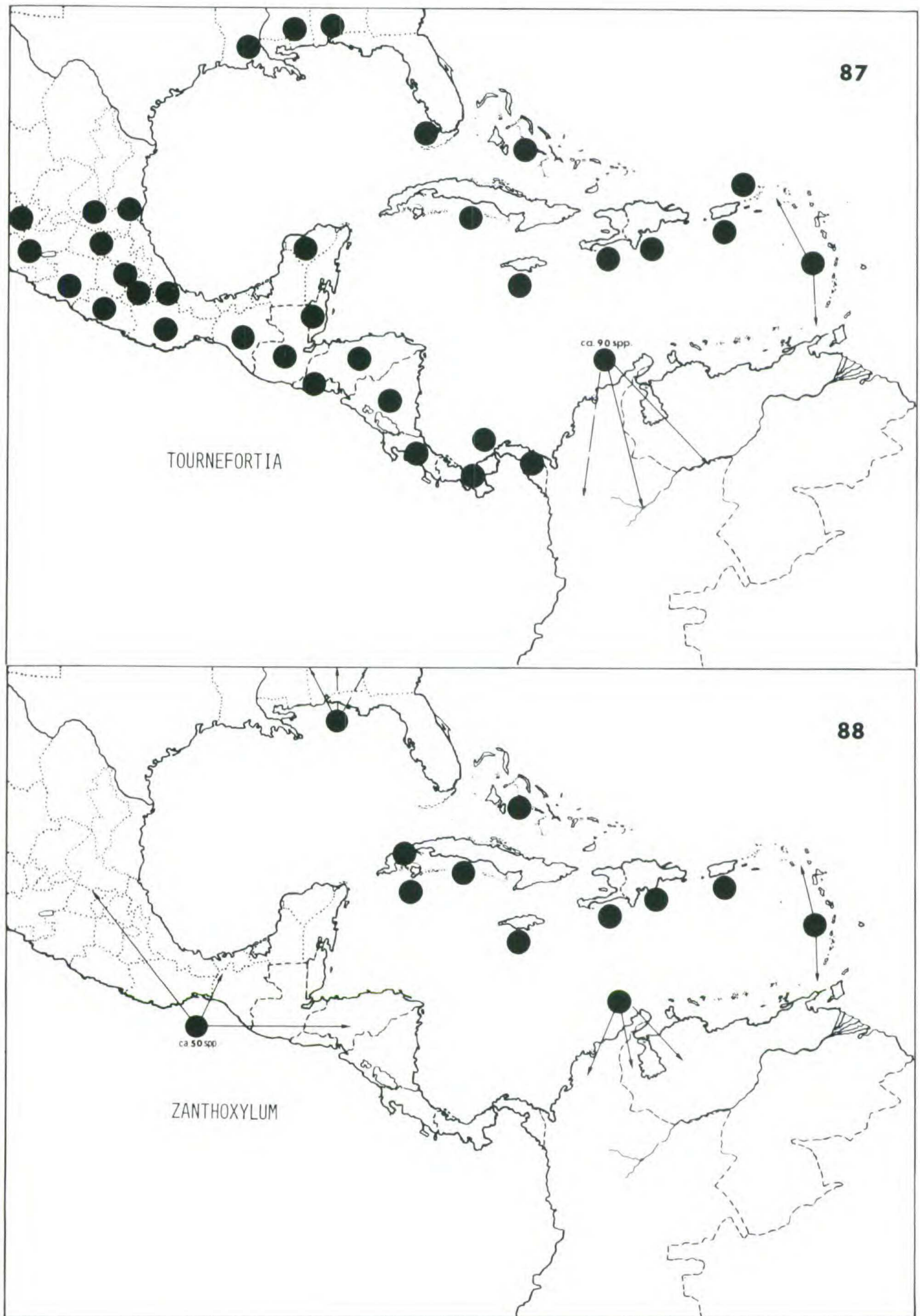
*Zanthoxylum* (Fig. 47–48)

The genus *Zanthoxylum* (Rutaceae) is a widely distributed assemblage of 20–30 species in temperate and subtropical regions (Fig. 88). At least seven species grow in Puerto Rico — *Z. flarrum*, *Z. caribaeum*, *Z. martinicense*, and *Z. monophyllum* being common. These medium-size deciduous trees (7–17 m tall) were common on Puerto Rico and adjacent islands, but because of their highly valued timber they are now scarce and restricted to protected forests (Little & Wadsworth, 1964). In its original habitat *Zanthoxylum* was widely distributed in the coastal limestone and lower montane forests, chiefly of western Puerto Rico. Gleason and Cook (1926) also reported the trees as common in mesophytic coastal forests.

Pollen of *Zanthoxylum* is present at Localities B and C with an abundance of 0.5–1.5%. Berry (1923, 1925, 1939) described *Fagara wadii* from the Miocene of Oaxaca, Mexico, and *F. miocenica* from Trinidad and Cuba. "The occurrence of species apparently transitional in the character of the perianth between *Zanthoxylum* and *Fagara* is ample reason to regard both as components of a single genus" (Brizicky, 1962b: 7). The genus *Fagara* is also listed as a synonym of *Zanthoxylum* in LaMotte's (1952) catalogue.

*Other Microfossils:* In addition to these genera, 120 other types were recovered. Many are referable to family, while others can only be placed in an artificial morphological category. Some of the forms represented are numerous fern





FIGURES 87-88.—Present Latin American distribution of genera identified from the San Sebastian (Oligocene) Formation, Puerto Rico.—87. *Tournefortia*.—88. *Zanthoxylum*.



spores similar to many genera of Polypodiaceae, about 15 types of palm pollen, and representatives of Bombacaceae, Burseraceae, Caryophyllaceae, Ericaceae, Euphorbiaceae, Gramineae, Magnoliaceae, Malpighiaceae, Nyctaginaceae, Oleaceae, Polygonaceae, Proteaceae, Rubiaceae, Theaceae, and Tiliaceae. Fungal spores were also common, but in the absence of adequate reference collections, and with little ecological data available for tropical fungi, identification and environmental interpretations were not possible (Graham, 1962a).

#### DISCUSSION

Initial studies of vegetational history in neotropical regions are likely to yield a miscellaneous assemblage of data difficult to integrate into a documented summary of paleoenvironments. Stratigraphic control and environmental trends established through studies of sequential fossil floras provide the necessary context for interpreting paleontological data, and this context is not available for northern Latin America. The San Sebastian assemblage is the only fossil flora known from the Antilles, and it is the only Middle Oligocene flora from Latin America for which recent published information is available. Until other studies are completed only qualified interpretations may be made of geologic events and vegetational response.

*New Fossil Records.*—One category of data from the Puerto Rican studies is reports of genera with no previous known fossil record. These include *Aetanthus* (Loranthaceae), *Bernoullia* (Bombacaceae), *Brunellia* (Brunelliaceae), *Corynostylis* (Violaceae), *Dendropanax* (Araliaceae), *Faramea* (Rubiaceae), *Hauya* (Onagraceae), *Jacaranda* and *Tecoma* (Bignoniaceae), *Marcgravia* and *Norantea* (Marcgraviaceae), *Pleodendron* (Canellaceae), *Rauwolfia* (Apocynaceae), *Tetrorchidium* (Euphorbiaceae), and *Tournefortia* (Boraginaceae). These 15 genera constitute 35% of the identified microflora.

*Oligocene Communities of Puerto Rico.*—Thirteen genera (ca. 30%) of the San Sebastian microflora no longer grow in Puerto Rico and represent extinctions after Middle Oligocene times. Three of these (*Norantea*, *Tetrorchidium*, *Bombax*) presently grow in the West Indies but not on Puerto Rico; two (*Aetanthus*, *Catosstemma*) are South American; two are Mexican and Central American (*Hauya*, *Engelhardia*<sup>4</sup>); and three occur in temperate regions of the eastern United States and eastern Mexico (*Fagus*, *Liquidambar*, *Nyssa*). The remaining three genera (*Bernoullia*, *Corynostylis*, *Pelliciera*) are widespread in Latin America except the Antilles. Changes in the composition of geofloras through time is common, particularly when ecologically comparable taxa are involved. With the exception of the cool-temperate element, these differences in composition between the San Sebastian microflora and the present vegetation of the West Indies do not imply significant climatic changes.

<sup>4</sup>A single collection is known from Colombia (D. E. Stone, personal communication, 1969).







that has been eliminated from the flora since Oligocene times. The other six genera were less common (0.5–2.5%). The third and climatically the most significant difference was the presence of a temperate to cool-temperate element (*Fagus*, *Liquidambar*, *Nyssa*). The presence of these plants is important in considerations of paleophysiography and will be discussed in a later section.

The gymnosperm element present today on extreme highlands in the Greater Antilles is absent from the microfossil assemblage. In the Dominican Republic the elfin or mossy forest is replaced at the highest elevations by a forest of *Pinus occidentalis*. In view of the prolific pollen production of pine, it is likely that pollen from such a community would be incorporated into the accumulating sediments. The only gymnosperm pollen recovered was a few grains of *Podocarpus* (Table 1). Hollick (1928) reports only *Zamia* from the megafossil flora of Puerto Rico. These data do not reveal the time of introduction of the high-altitude gymnosperm element in the Antillean flora, but this apparently took place in post-Oligocene times.

In addition to the microfossils, Hollick (1928) reported 56 genera of megafossils from the Collazo Shales (Table 4). Several were tentative identifications, and others need verification. Consequently the present megafossil record is of limited use in environmental reconstructions. Pollen of six megafossil genera was recovered (*Hemitelia*, *Chrysophyllum*, *Eugenia*, *Guarea*, *Malvocarpon* [cf. *Abutilon*], and *Rhizophora*), and others (*Bactris*, *Palmacites*, *Palmocarpon*, *Cassia*, *Inga*, *Sophora*) may be among microfossils presently identified only to family (Palmae, Leguminosae). However, the reliability of the megafossil record cannot be established nor comparisons made between the mega- and microflora until the megafossil flora has been revised; at present only 10% of the megafossil genera was found as microfossils.

TABLE 4. Genera of megafossils from the Collazo Shales, Puerto Rico (Hollick, 1928). Asterisk (\*) indicates genus also represented by pollen.

Algae	<i>Copaiva</i>	<i>Musophyllum</i>
<i>Chondrites</i>	<i>Cynometra</i>	<i>Myrcia</i>
Ferns and Allies	<i>Dipholis</i>	<i>Myrsine</i>
* <i>Hemitelia</i>	<i>Echites</i>	<i>Oreodaphne</i>
<i>Isoetes</i>	<i>Echitonium</i>	<i>Palmacites</i>
Gymnosperms	* <i>Eugenia</i>	<i>Palmocarpon</i>
<i>Zamia</i>	<i>Ficus</i>	<i>Palmophyllum</i>
Angiosperms	* <i>Guarea</i>	<i>Pithecellobium</i>
<i>Acroclidium</i>	<i>Guettarda</i>	<i>Plumiera</i>
<i>Aniba</i>	<i>Hancornia</i>	<i>Protorhipis</i>
<i>Annona</i>	<i>Hufelandia</i>	<i>Psidium</i>
<i>Apocynophyllum</i>	<i>Icacorea</i>	<i>Ramulus</i>
<i>Aspidosperma</i>	<i>Inga</i>	* <i>Rhizophora</i>
<i>Bactris</i>	<i>Iriartea</i>	<i>Sapindus</i>
<i>Cassia</i>	<i>Juglans</i>	<i>Sapota</i>
* <i>Chrysophyllum</i>	<i>Lonchocarpus</i>	<i>Sideroxylon</i>
<i>Coccoloba</i>	* <i>Malvocarpon</i>	<i>Sophora</i>
<i>Combretum</i>	<i>Manicaria</i>	<i>Stylogyne</i>
	<i>Melicocca</i>	<i>Trichilia</i>
	<i>Misanteca</i>	<i>Zizyphus</i>



*Oligocene Climates and Paleophysiography.*—In the preceding section it was noted that about 75% of the identified Oligocene flora presently grows in the West Indies. Of the 13 genera no longer present, 10 grow in habitats similar to those available on Puerto Rico. Consequently the Oligocene climates and general environmental conditions must have been comparable to those of the present. These conditions include an insular environment, although considerably greater in extent than the present landmass of Puerto Rico; a central highland with greater relief than at present; trade winds from the northeast during the winter months, shifting to the east and southeast by July; a rainfall near 180 inches on the windward slopes with a rainshadow effect reducing annual precipitation locally to near the present 10 inches to the lee; and a mean annual temperature of about 78° F on the south coast to several degrees less than the present 70° F in the mountains.

The most significant difference between the Oligocene communities and those of the present was the temperate element in the fossil flora. If Oligocene climates in the Antilles were comparable to those of today, accounting for the distinct similarities between past and present vegetation, physiographic relief must have been greater. The higher altitudes provided the temperate environments required by *Fagus*, *Liquidambar*, and *Nyssa*, without altering conditions necessary for the growth of more tropical species.

An estimate of physiographic relief in the Greater Antilles during the Oligocene may be made from two kinds of evidence. One is on the basis of the vegetation on present highlands compared to those required by the temperate fossil communities. The highest present elevation on Puerto Rico is Cerro de Punta, 1,338 m, where the vegetation is an elfin or mossy forest (Howard, 1968). In Cuba the highest elevation is Pico Turquino, about 2,000 m. The vegetation there is similar to that on Cerro de Punta. The highest altitude in the Greater Antilles is Pico Duarte, 3,175 m, in the Dominican Republic. The vegetation of Pico Duarte (Holdridge, 1945; G. I. Gastony, personal communication, 1969) is a rocky, windswept, open community of *Pinus occidentalis* with festooning lichens reminiscent of the elfin forest at lower elevations. Other plants at the summit include *Pellaea ternifolia*, *Plagiogyra semicordata*, *Lobelia ekmanii*, *Scrophularia densifolia*, *Hypericum pycnophyllum*, *Gnaphalium eggertii*, *Dendropemon pycnophyllum* (parasitic on pines) and *Lyonia heptamera*. The vegetation on other Antillean highlands has been described by Asprey and Robbins (1953; Jamaica), Howard (1968; Puerto Rico), Seifríz (1943; Cuba) and Urban (1909–1910). Several widespread temperate genera are mentioned: *Apium*, *Aster*, *Bidens*, *Clematis*, *Clethra*, *Drosera*, *Eupatorium*, *Hypericum*, *Ilex*, *Myrica*, *Oxalis*, *Potentilla*, *Ranunculus*, *Rubus*, *Smilax*, *Vaccinium*, *Viburnum*, and others. Absent from this assemblage of herbs, shrubs, and small trees are the larger arboreal forms found in the fossil deposits.

If it is assumed that altitudes greater than at present provided habitats for the growth of a cool-temperate element in an insular environment at 18° N latitude, the mountains of the Greater Antilles during the Lower and Middle Tertiary exceeded 3,175 m (10,300 feet). Erosion and differential subsidence reduced these



heights with concomitant elimination of the cool-temperate habitats. The low percentages (0.5–4.5%) of the arboreal temperate element in the fossil deposits are consistent with the hypothesis that this element grew in a highland habitat removed from the basin of deposition.

In evaluating the possibility of Oligocene highlands that were of significantly greater altitude than those of today, it must be noted that *Fagus*, *Liquidambar*, and *Nyssa* all presently grow in east-coastal Mexico, most commonly at elevations of about 1,800 m (6,000 feet). This is a continental rather than insular environment, however, which is not as affected by the Guiana-Caribbean-Florida Gulf Stream current. Further, although these floristic data may only suggest the possibility of Oligocene highlands greater than 3,175 m, this estimate of paleo-physiographic conditions in the Greater Antilles is supported by recently available geologic data. The following information has been provided by R. P. Briggs, U.S. Geologic Survey, San Juan.

There is no good evidence for the existence, prior to the middle or late part of the Late Cretaceous, of any sizable islands or landmasses in this part of the crust of the world. From that time probably through the middle Eocene some reasonably good-sized islands may have been present, but nothing approaching the size of Puerto Rico today, rather perhaps more of the order of some of the Virgin Islands.

After the middle Eocene there was great crustal uplift, forming a landmass considerably greater than exists today, something perhaps approaching 100 miles north to south and surely connecting with the Virgin Islands on the east and probably with Hispaniola on the west. It is quite possible that elevations on this landmass approached 15,000 feet.

This estimate is based as follows. An oil test well on the north coast of Puerto Rico revealed the middle Tertiary San Sebastian Formation resting on an eroded volcanic basement at a depth presently about 5,500 feet below sea level. The present highest point on Puerto Rico is 4,390 feet. This gives a present elevation of Cerro de Punta, above the eroded basement, of a little less than 10,000 feet. Our evidence though shows that there probably was differential subsidence, with the coastal area subsiding somewhat more than the present interior area. But, considering later erosion and the fact that the unconformity probably goes to somewhat greater depth northward beneath the Atlantic Ocean, I would not be surprised if there were 10,000 feet of relief at the time of deposition of the Middle Tertiary rocks in the test well. Perhaps there was a considerably greater relief at the maximum time of uplift, probably in the late Eocene.

You estimate the maximum altitude of Puerto Rico during the middle Oligocene to have been between 6,500 and 7,000 feet above the sites sampled. If we average the present elevations of your sites to 1,000 feet and the average highlands of Puerto Rico to about 4,000 feet, it would appear you are thinking in terms of 3,500 to 4,000 feet of post-middle Oligocene erosion. Going back to my oil test well *versus* present relief estimate, this certainly would seem to make your estimate and my estimate similar. That is 1,000 feet plus 6,500 feet plus 5,500 feet equals a minimum altitude of 13,000 feet.

Of course, much of what I said above is grossly oversimplified, and there is evidence for differential subsidence. Despite this, I think it is safe to say that the relief of ancestral Puerto Rico from Late Eocene to Middle Oligocene time was appreciably greater than exists today. It is also fair to say it was being degraded at a very fast rate.

A comparison of Table 1, Localities A and B with Fig. 4 reveals other details of the vegetation, physiography, and some facies control of the microfossils. At Locality A (second column, Table 1) all identified genera are represented at 2.5% or less except *Rhizophora* which constitutes up to 96% of the microflora. This site marks the approximate position of the shoreline during the Middle



Oligocene bordered by a mangrove swamp of *Rhizophora mangle* and *Pelliciera rhizophorae* (the highest percentages of the latter were also found at Locality A).

Samples 19, 25, and 40 from Locality B (Fig. 4) are coalified lignites, and *Rhizophora* pollen makes up 61–77% of the samples. Samples 15 and 33 are clays (high mineral content), *Rhizophora* pollen constitutes 1% of sample 15 and was absent from sample 33. The alternate layering of organic-rich *versus* mineral strata indicates the shoreline was vacillating, probably in response to gradual short-term pyrogenic (rather than eustatic) changes. During the times of subsidence mangrove vegetation dominated at Locality B and the developing soils incorporated a large amount of organic material. With slight and gradual short-term emergence the site was drained, *Rhizophora* was eliminated at its inland boundary, and more upland vegetation became established on soils of greater mineral content. One of the plants commonly approaching sites vacated by the mangroves was *Engelhardia*. At each locality it increased considerably more than other species as *Rhizophora* decreased (e.g., from a maximum of 3% where *Rhizophora* is abundant to 54% where it is scarce). The reciprocal relationship in percentages of *Rhizophora-Pelliciera* and *Engelhardia* pollen reflects the structural instability of the Oligocene shoreline and records the response of these communities to the orogenic changes characterizing the Caribbean Basin during Middle Tertiary times.

*Pathways of Migration.*—Equatorial climatic belts are known to have extended considerably beyond their present limits during the Early and Middle Tertiary. The Eocene Goshen flora of western Oregon, near latitude 44 degrees north contains a significant tropical element (Chaney & Sanborn, 1933), and even the revised Tertiary floras of Alaska are yielding some species of tropical affinities (Wolfe, personal communication, 1969). Geological evidence from the Antilles reveals the presence of larger and more continuous landmasses (lessening the physical, oceanic barrier to migration), and paleobotanical data reveal climatic conditions favorable to the interchange of northern and southern elements. That many southern species actually did extend into the southeastern United States is evident both from paleobotanical studies of Mississippi Embayment floras and floristic affinities of the modern communities (Graham, 1965*b*). The question is whether the Antillean Arc or the Isthmian-coastal Mexico region was the principal migration route between the North and South American biotas during Early Tertiary times. Data from Puerto Rico make possible some preliminary speculations, although results from our studies in Panama and Veracruz, Mexico, may require revision of these.

If ancestral Puerto Rico was a landmass some 100 miles wide and included at least the Virgin Islands, Puerto Rico, and Hispaniola, the sea barrier between the West Indies and the southeastern United States may seem significantly reduced. However, the Tertiary seas extended northward across at least part of peninsula Florida, and Oligocene strata are exposed in southern South Carolina, Georgia, Alabama, Mississippi, and as far as 120 miles inland along the Texas coast (Fig. 89). In eastern Mexico and the Yucatan Peninsula, the closest point between Mexico and the Antilles (Cuba), the inland extent of Oligocene seas was



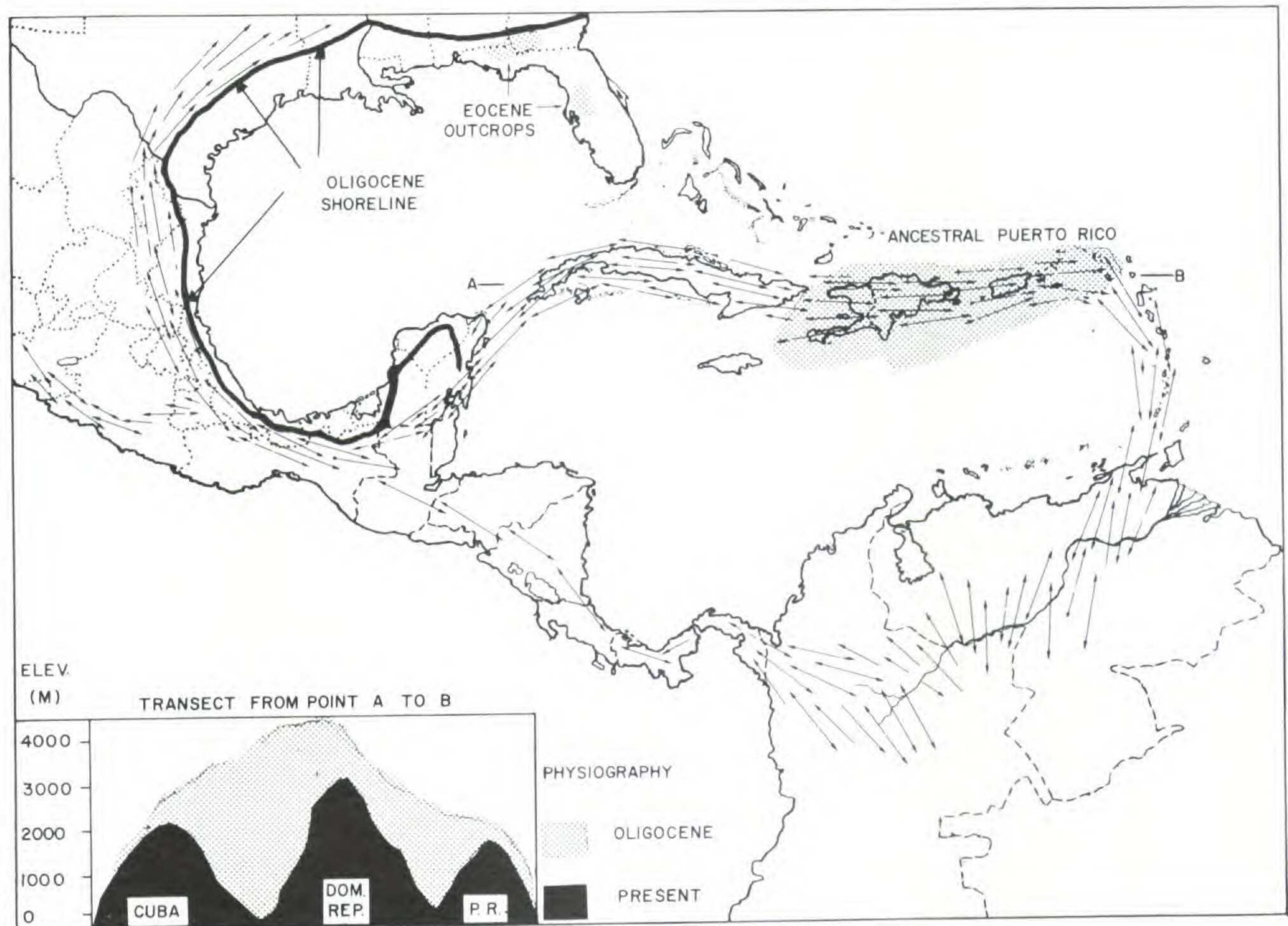


FIGURE 89.—Paleogeography and Caribbean migration routes during the Middle Oligocene.

considerably less (Salas, 1968). The maximum dimensions of ancestral Puerto Rico, its east-west connections (*viz.*, with Cuba, Yucatan, and the Lesser Antilles), and the history of other islands in the Caribbean are not well known, but available evidence suggests the physical barrier between the southeastern United States and the Greater Antilles during the Middle Oligocene was probably more extensive than at present; between the Greater Antilles and Mexico it probably was no greater than at present and possibly less.

A second approach to evaluating the Antilles as a Tertiary landbridge is by analysis of the floristic affinities of the Oligocene vegetation. Fourteen genera of the Puerto Rican Oligocene flora no longer grow in the West Indies. All 14 are Mexican (commonly eastern Mexican), Central and northern South American. Those genera which may appear to reflect affinities with the eastern United States (*Fagus*, *Liquidambar*, *Nyssa*) also grow in Latin America (*e.g.*, eastern Mexico). The same would hold if Hollick's (1928) identification of *Juglans* were included. Thus the 44 identified genera of the San Sebastian Oligocene flora all have affinities with northern Latin America, and none have exclusive affinities with the southeastern United States.

On the basis of these geological and botanical considerations a preliminary model may be made of Tertiary migrations along the Caribbean Basin (Fig. 89). The time of maximum extent of tropical climates (Early Tertiary) corresponds with the period of extensive uplift and maximum availability of land surface in



the Antilles. In the absence of both physical and climatic barriers, two migration routes were available for extension of tropical and subtropical species into northern regions—the Isthmian-coastal Mexico route and the Antillean Arc. Those species migrating along the former were able to extend into southern United States (*cf.* genera listed by Ball, 1931, 1939; and Berry, 1916 from Eocene deposits). After Middle Oligocene times these tropical elements either became extinct as a result of climatic trends toward cool-temperate conditions, evolved new ecotypes capable of growing under temperate environments (*e.g.*, *Dirca*, Thymelaeaceae; *Asimina*, Annonaceae; *Diospyros*, Ebenaceae) or survived in subtropical outliers such as the southward expanding Florida peninsula (*e.g.*, *Rhizophora*, *Laguncularia*, *Tillandsia*, *Avicennia*, *Annona*, *Dipholis*; Graham, 1965*b*).

The interchange of species along the Antillean Arc between South America and east coastal Mexico (Yucatan) was facilitated by greater landmasses and physiographic diversity which provided an array of habitats. Further northward migration was hindered, however, by an oceanic barrier at least as extensive as at present. Regarding the Bahama Islands which presently form the nearest complete connection between the Greater Antilles and southeastern United States, Butterlin (1956: 173) states that from the Lower Cretaceous “until the Quaternary, shallow calcareous sedimentation consisting of reef or inter-reef formations were established in the marine subsidence basin. The area remained out of the scope of the orogenic forces and these series are not folded. During the Quaternary and particularly the Pleistocene, relative movements of the marine level and submerged shelf have enabled the latter to emerge.”

Reconstruction of the geologic history of the Florida peninsula is complicated by Pliocene and younger strata overlying the Lower and Middle Tertiary deposits. Much of the pertinent data must come from studies of subsurface geology based on available well cores. According to the correlation charts of Cooke, Gardner, and Woodring (1943) the Ocala, Byram, and Suwannee Limestones are marine units deposited during Upper Eocene through Middle Oligocene times. Further, the Suwannee Limestone is encountered in subsurface cores as far north as Fort Pierce, and isopach maps (Toulmin, 1955) show that it thickens to the south. These data mean that at least the lower one-third of the Florida peninsula was submerged during much of Eocene and Oligocene times.

In the vicinity of Ocala, Florida, and in the northern Florida-Georgia region exposed Eocene strata are surrounded by younger rocks. Geologically this could mean these areas were emergent during Middle and Late Tertiary times and no younger overlying rocks were deposited. According to this interpretation these areas would be islands, and their presence would reduce the oceanic barrier between the Antilles and the southeastern United States. Another possibility is that the Eocene units were not emergent during post-Eocene times but have been exposed through erosion of the overlying beds. The Eocene rocks in question form the cap of the Ocala Uplift. The association of the beds with a geomorphic feature of positive relief favors the latter interpretation. According to Stringfield (personal communication, 1969) the outcropping of the Ocala Limestone is an erosion feature and not due to continuous post-Eocene emergence. In summary, the geological



evidence indicates that much of peninsula Florida was submerged and no intervening islands were present during the time the floristic composition of the San Sebastian flora was developing.

In contrast, the Lesser Antilles, forming the present connection between the Greater Antilles and northern South America, were probably significant landmasses during much of the Tertiary. According to Butterlin (1956) "the Dutch islands must have remained above water (from Cretaceous) until the Upper Eocene. During that last period the sea flooded the region depositing limestones and marls. . . . The islands reemerged again and the sea did not flood the area until the Miocene."

As a consequence of the difference in physiographic history between the northern and southern connections of ancestral Puerto Rico, the Oligocene communities include numerous elements common to the present plant associations of eastern Mexico, Central and northern South America, and are floristically distinct from the vegetation of the southeastern United States. The herbaceous and shrubby temperate elements in the modern Antillean flora, including many species with broad ecological tolerances, constitute either holdovers from older Tertiary times (the distinctly cool-temperate arboreal forms being eliminated through erosion of the highland habitats) or modern introductions through natural, long-distant dispersal and anthropogenic factors.

#### SUMMARY

In the preceding section a model has been presented for early Tertiary migration patterns around the Caribbean Basin (Fig. 89). The model is consistent with paleobotanical and geological data as presently understood, but it can also be evaluated on the basis of natural (*i.e.*, non-anthropogenic) distribution patterns of modern organisms. We accept as a generalization that animal, particularly land vertebrate, distribution is influenced to a considerable extent by the range of the plants serving as a source of food and protection. If this is true, and if the model is essentially correct, certain plants and animals should have at least vestiges of a distribution pattern consistent with Fig. 89. The organisms exhibiting this pattern should be 1) those whose origins date back at least to Early or Middle Tertiary times, and 2) those with conservative distribution potentials and without exceptionally broad ecological tolerances (*e.g.*, non-weedy species). Changes in the range of such organisms can be expected to commonly reflect changes in the physical and/or climatic barriers to migration.

Based on the model, plant and animal species of the southeastern United States having affinities with Latin America should show strongest affinities with eastern Mexico and/or Central America and/or northern South America, rather than with the flora and fauna of the Antilles even though the latter is geographically closer. Although the literature of biogeography can be surveyed for examples pertinent to evaluating the model, critical tests can only be made by specialists in various groups who can differentiate between biologically meaningful patterns and those created by poor taxonomy. One range reflecting the expected pattern is that of the plant genus *Cuphea* (S. Graham, personal communication, 1969). The spe-



cies occurring in the southeastern United States are generally more closely related to those of Mexico, Central and even northern South America than to those presently growing in the Antilles. Similarly several genera of trees in the eastern deciduous forest of the United States occur disjunct in eastern Mexico and regions to the south and are absent in the Antilles. Martin and Harrell (1957) cite similar patterns among the vertebrates.

A final consideration relates to the history of the isthmian region during lower Tertiary times. Studies on the vegetational history of Panama are just beginning, but according to Woodring (personal communication, 1969) study of the geology and fossil faunas reveals that the area was submerged during at least the major part of the Tertiary (from Paleocene to Early Pleistocene). At present it is not possible to determine the effectiveness of the oceanic barrier to interchange between the terrestrial plant communities to the north and south. It seems reasonable, however, considering the relatively emergent condition of the Antillean Arc and east-coastal Mexico region compared to the Isthmus, that the former may have served as the principal migration route between the North and South American biotas during the Tertiary.

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